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EFFECTS OF SPACE SHUTTLE EXHAUST PLUMES ON GILLS OF SOME ESTUARINE FISHES: A LIGHT AND ELECTRON MICROSCOPIC STUDY

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ABSTRACT The first few launches of the space shuttle resulted in fish kills in a lagoon near the launch site. To study this phenomenon further, sheepshead minnow (*Cyprinodon variegatus*), sailfin molly (*Poecilia latipinna*), and mosquitofish (*Gambusia affinis*) were exposed to the exhaust plume in buckets placed near the launch site. An open bucket provided a full exposure, a partly closed one provided an intermediate exposure, and a closed one was the control. Three h after launch, the pH of the water from the full exposure had decreased from about 7 to about 3, Al and Fe levels had increased, and some fish had died. Gills of most fishes from full exposures and some from intermediate exposures were damaged. Gills, however, exhibited no aneurysms, mucus coagulation, or hemorrhaging. Some secondary lamellae swelled, some fused with adjacent lamellae, and others clubbed or retracted into the filament. Many lamellar pavement cells died and sloughed off. Mucous cells of intermediate exposure specimens bulged on the filament surface and pavement cells lost their microridges. Mineral deposits, probably aluminum oxide, occurred on gills of fishes from full exposures. Focally, pavement cells were eroded exposing the underlying structures. The sudden pH drop in the full exposures probably caused the gill damage. However, we could not determine the effect of previous exposure on the experimental fish, or whether gill damage was the lethal lesion. The possibility is indicated that some fish recover after exposure to the exhaust plume.

INTRODUCTION

Kills involving fewer than one hundred small fish occurred in a lagoon following each of the first three launches of the Space Transportation System (STS; space shuttle) from Kennedy Space Center, Florida, USA. The cause of the fishes' deaths was not determined but was suspected to be gill damage resulting from a sudden drop in pH caused by the exhaust plume generated by the solid rocket boosters (Milligan and Hubbard 1983). Our preliminary histopathological examinations of whole fishes that were exposed to the exhaust plume of STS-4 in June 1982 confirmed those observations. We, therefore, designed an experiment to study further this unique interface between technology and estuarine ecology where an extreme stress condition develops and disappears rapidly. Our primary interest involved the effects of toxic agents or conditions on tissues, especially gills, of fishes exposed to the exhaust plume. In the present study, we examined whole fishes exposed to the space shuttle exhaust plume by light microscopy and gills by light microscopy, transmission electron microscopy, and scanning electron microscopy.

MATERIALS AND METHODS

Species studied included the mosquitofish *Gambusia affinis* (Baird and Girard); sailfin molly *Poecilia latipinna* (Leseur); Gulf killifish *Fundulus grandis* Baird and Girard; and sheepshead minnow *Cyprinodon variegatus* Lacépède. Two experiments were conducted in which fish were exposed to the exhaust plume: one during the launch of STS-4 in June 1982 and another during the launch of STS-5 in November 1982. To determine if previous exposure to the exhaust plume affected a fish's subsequent exposure, the species named above were collected from two sites, Molly Pond and an unnamed lagoon. Molly Pond (temperature 25°C, salinity 4 ppt), situated 6100 m and 260° west-southwest from the launch platform, was previously unaffected by shuttle launches. The lagoon (25°C, 14.5 ppt), a man-made body of water 400 m north from the platform, was the site of previous launch-related fish kills. For acclimatization, fish were transferred to two 75.7 liter aquaria with water temperature adjusted to 23–24°C and salinity to 10 ppt adjusted upward with Instant Ocean® and downward with deionized water. Artificial light hours occurred from 0800 to 1700 h daily. Fish were maintained 12–19 days before the experiment on a diet of TetraMin® flakes once each morning. Stressed fish were removed.

Fifteen and one-half h before the launch, fish were transferred to plastic buckets containing 10 liters of deionized water adjusted to 10–12 ppt. Five buckets contained 12 fish, one contained 10 fish, and each bucket included specimens of all three species. One set of buckets contained fish from Molly Pond and the other from the lagoon. In each set, one bucket was protected from the exhaust plume by a plastic cover (control exposure), one was open to the plume (full exposure), and one was covered with cheese cloth to provide a partial exposure (intermediate exposure). The buckets were placed 10–15 meters north of the pad perimeter fence, 3–4 meters west of the lagoon. This site is about 445 m north of the launch pad in a direct line with a concrete-lined flame trench that channels much of the exhaust plume away from the platform.

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TEXT-FIGURE 1

Water chemistry data from STS-5 fish experiment.

Exposure Specimen Source	pH	Temp (°C)	D.O.	Salinity (ppt)	AL (mg/l)	Fe (mg/l)
Control	–	–	–	–	<0.2	0.33
Closed						
Molly Pond	7.2	24.0	5.8	10.0	<0.2	0.22 ± 0.01
Lagoon	7.2	22.5	6.2	9.5	<0.2	0.2 ± 0.0
Intermediate						
Molly Pond	4.7	22.0	6.2	10.5	0.4 ± 0.0	0.58 ± 0.01
Lagoon	4.8	22.0	5.6	10.5	0.5 ± 0.0	0.75 ± 0.0
Open						
Molly Pond	2.9	21.0	6.0	10.0	0.8 ± 0.0	1.25 ± 0.07
Lagoon	2.8	22.0	6.0	11.0	1.3 ± 0.0	1.6 ± 0.0

Access to the experimental site was gained within 1.5 h after launch. Temperature, pH, conductivity, dissolved oxygen, and salinity of water were measured from each bucket. Water samples for heavy metal analysis by atomic absorption spectrophotometry were collected and placed on ice. Whole fish were fixed in 10% formalin. Specimens from which gills would be removed for ultrastructural examination were placed on ice to be dissected and fixed 5.5 h later. Gill arches, neither the first nor the last, were removed and fixed in ice-cold 3.0% phosphate-buffered glutaraldehyde for 3 h then placed in cold 0.1 M phosphate buffer and shipped on dry ice to Ocean Springs, Mississippi, for further processing and analysis which commenced 48 h later.

For transmission electron microscopy, gill arches were cut into small pieces, postfixed in 1% osmium tetroxide for 2 h and dehydrated in ethanol. After treatment with propylene oxide, the tissues were embedded in epoxy resin. For orientation and further light microscopical analysis, 1-micron thick sections were cut on an LKB ultramicrotome, mounted on glass slides, and stained with toluidine blue. Thin sections were cut on glass knives, collected on uncoated copper grids, stained with uranyl acetate and lead citrate, and examined in a Siemens 1A electron microscope.

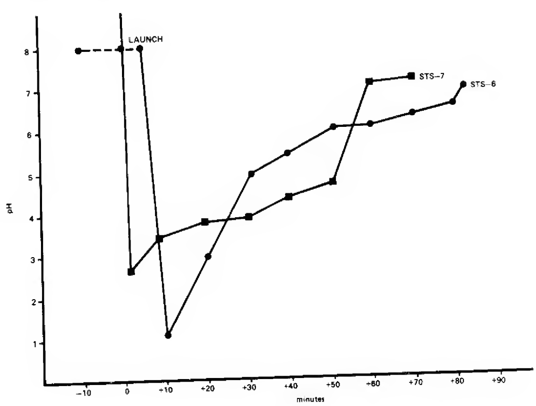
RESULTS

General Observations and Physical Parameters

The exhaust plume from each of the first five STS launches affected an area near to and north of the launch pad. A strong acidic odor, probably HC1, lingered and aluminum oxide powder covered much of the vegetation and together with dust blown from the launch gave the surface of the lagoon a tannish tint. Dead fish were usually found in dense grasses at the southern end of the lagoon in 15–30 cm of water.

Text-figure 1 shows water chemistry data from the six experimental buckets. Temperature, dissolved oxygen, and salinity changed little, if any, in the intermediate and full exposures. Aluminum and iron content increased about 2 to 4 times. There were no differences in the levels of other metals including Cd, Cr, Cu, Mn, Ni, Pb, and Zn. The pH, initially 7.2 in water from both the Molly Pond and the lagoon, decreased to 2.9 in the full exposure from Molly Pond and to 2.8 in the full exposure from the lagoon. Continuous pH measurements from two succeeding launches were recorded. The pH of the lagoon was between 8 and 9 before the launch and dropped to about 1 within 2–3 minutes following ignition (Text-figure 2). Within 60 minutes, the pH of the lagoon had recovered to about 7. In the Molly Pond full exposure, 2 of 12 specimens died, whereas 9 of 10 died in the lagoon full exposure.

Histopathological examination of paraffin-embedded whole fish revealed considerable damage involving gills but little, if any, involving olfactory, nervous, integumentary digestive, and hemopoietic tissues. Studies of peripheral



Text-figure 2. This graph represents continuous pH values taken during the launch of STS-7. The site was in the lagoon north of the launch pad. Water depth was 12 centimeters and pH was monitored at approximately 6 centimeters.

blood were not conducted, but blood in tissues other than gill did not appear affected. Since the gill appeared to be the major target organ, it was chosen for more extensive study.

Gill Morphology of Control Fish (Closed Bucket)

Gills of all three species appeared typical for teleosts at the organ, tissue, cell, and organelle level as seen by light microscopy (LM) and transmission electron microscopy (TEM) (e.g., Laurent and Dunel 1980), and in surface morphology as seen by scanning electron microscopy (SEM) (e.g., Hossler *et al.* 1979a). Most observations were made by LM of paraffin and epoxy-embedded specimens and by SEM. Sectioning difficulties caused by mineral deposits which occurred in interlamellar spaces of fish from intermediate and full exposures made TEM observations difficult to achieve. Observations could be made on broad areas of tissue but not on individual cells.

Gills of Molly Pond and lagoon fishes from control exposures showed no damage that might have indicated previous exposure to toxic conditions. Secondary lamellae were usually straight and interlamellar spaces free of deposits (Plate 1, Figures 1, 2). A narrow lymphatic space separated the smooth pavement epithelial layer from the underlying intralamellar capillaries. Red blood cells were normal. Short, irregular projections arose from lamellar pavement cells of some specimens. Filaments of control gills contained undifferentiated cells, mucous cells, and chloride cells and often exhibited large, apparently intercellular, spaces. Mucous cells were especially numerous on the filament surface associated with the efferent artery whereas chloride cells were abundant near the filament surface associated with the afferent artery and in interlamellar regions (Plate 1, Figure 3). Chloride cells stained lightly and had basally-situated nuclei. The identity of chloride cells was confirmed by TEM. Most chloride cells appeared to have deep apical pits opening to the filament surface.

Gill lamellae of control specimens were thin, regular, overlapping plates with relatively smooth surfaces without pores or microridges (Plate 1, Figure 4). The filament surface, however, had numerous pores, the majority of which probably represent apical pits of chloride cells. Microridges were usually absent from the center of pavement cell surfaces, but abundant near the peripheries (Plate 1, Figure 5).

Changes in Gills of Fishes from Intermediate Exposures

Secondary lamellae showed no disruption or erosion, but some were angulated (Plate 2, Figure 6) and swollen. None of the fish died and no conspicuous differences in the types of pathological changes occurred among species. Some lamellae appeared thickened and retracted into the filament (Plate 2, Figure 7). Secretory granules of some mucous cells on interlamellar regions of filaments were denser than in others. Mucous cells moved to the surface and appeared to bulge outward (Plate 2, Figure 8). Interlamellar spaces of some fish had mineral deposits that ranged from granules less than 1.0 μm in diameter to aggregates more than 40.0 μm in diameter. Pathological changes in gills, however, did not relate to the presence of granules.

Numerous broad, shallow depressions and some deeper ones occurred near the interlamellar region (Plate 2, Figure 9). Mucous cell surfaces were usually smooth but sometimes had small granules (about 0.5 mm in diameter) attached (Plate 2, Figure 10). Such granules occurred often on pavement epithelial cells, especially microridged portions. Little change occurred in the microridge patterns of the pavement epithelial cells.

Changes in Gills and Other Organs of Fish from Full Exposures

Histopathological changes varied among specimens, arches, and filaments, often involved small portions of a few lamellae, and ranged from apparently mild to potentially lethal ones.

Histopathological changes exhibited in some dead specimens that had not autolyzed appear relevant. In a few paraffin-embedded specimens that exhibited severe gill necrosis and had died following the exposure, blood spaces of the heart, particularly the atrium, were congested and the pericardial cavity filled with a transudate (Plate 3, Figure 11).

Only one of four fish, a sailfin molly, from full exposures examined in epoxy-resin sections had not died following the exposure. In this fish, secondary lamellae shortened and epithelial cells lifted away from underlying tissues creating broad lymphatic spaces (Plate 3, Figure 12). Mineral deposits occurred in many interlamellar spaces. Apices of mucous cells lay near the surface of the nonlamellar portion of the filament, and many mucous granules stained less densely with toluidine blue than did those from control or intermediate exposures (Plate 3, Figure 13). Changes in gills of fish that died in full exposures included fusion of adjacent lamellae, clubbing of the ends of lamellae, hemostasis in afferent and efferent filament vessels and in lamellar capillaries, and erosion of cells of secondary lamellae (Plate 3, Figure 14). TEM confirmed that the eroded cells were pavement epithelial cells (Plate 3, Figure 15).

Focal lesions involved primarily lamellae in the distal two-thirds of filaments (Plate 4, Figure 16). In some places, the surface epithelium eroded away exposing the underlying filament vessels and lamellar capillaries (Plate 4, Figure 17). Mineral deposits occurred frequently. Neither microridges nor pores were often seen on filaments of these fish (Plate 4, Figure 18).

Fish that died in full exposures exhibited many of the changes seen in fish that had not. This included erosion of epithelial layers. Lamellae in these fish frequently fused. Plate 4, Figure 19 shows a small area of lamellae exhibiting several degrees of fusion. In some places, fusion occurred between broad areas of epithelium and, in other places, among individual cells. Numerous bulges in the lamellae probably represent nuclei of pavement epithelial cells.

DISCUSSION

Few field studies have been conducted to determine the ultrastructural effects of toxicants on fishes. Optimally, specimens for such studies are collected, fixed, and processed rapidly. Hughes et al. (1978, 1979) developed morphometric techniques for determining subtle effects of pollutants on fish gills and emphasized the importance of consistent and appropriate fixation and processing protocols for specimens used for morphometry. In our study, logistical problems including delayed access to the experimental site, a delay in fixation (although specimens were kept on ice), and a delay in processing caused by having to ship the tissues to a second laboratory were unavoidable. Such factors could obviate morphometrical analyses but not qualitative ones, providing adequate control specimens are examined. Even examination of dead specimens can give useful information.

All experimental fish exposed to the exhaust plume had severely damaged gills. Damage consisted mainly of necrosis and sloughing of pavement cells of secondary lamellae. Other histological changes included swelling and clubbing of secondary lamellae, loss of microridges from the filament pavement cells, and mucus secretion. These changes were probably caused by sudden exposure to acid conditions as recorded in buckets exposed to the exhaust plume. Additional measurements taken during the launches of STS-6 and STS-7 confirmed this pH decline in the lagoon near the experimental site. The ignition of the two solid rocket boosters and the simultaneous release of several thousand kiloliters of deluge water result in the formation of gases and particulates including carbon dioxide, aluminum oxide, water vapor, hydrogen chloride, and iron chloride. Hydrogen chloride gas mixes with the ambient air and is readily scavenged by atomized water droplets and small drops which form from condensation as the exhaust plume cools. Most of the larger drops, possessing a pH of less than 0.5, are deposited near the pad (Keller and Anderson 1983). Our study indicates that exhaust plume components exert their primary histopathologic effects on gills of exposed fishes. This confirms an earlier preliminary study by Milligan and Hubbard (1983).

Accurate diagnosis of gill effects must be based on examination of large numbers of filaments because effects vary widely in different parts of a gill arch (Fromm 1980). SEM can help overcome some of these sampling problems and, when used in combination with LM and TEM, rather fine changes can be determined in specific cell types such as pavement epithelial cells, chloride cells and mucous cells.

Some subcellular aspects of the histopathological response of gills to toxic conditions deserve comment. Filament pavement cells of *G. affinis, C. variegatus,* and *P. latipinna* had microridges, but those on secondary lamellae did not. Similarly, Hossler et al. (1979a) reported that secondary lamellae of mullet *Mugil cephalus* Linnaeus lacked microridges. Microridges, however, were reported on secondary lamellae of the catfish *Heteropneutes fossilis* (Bloch) by Rajbanshi (1977), and the dogfish *Scyliorhinus canicula* Linnaeus by Crespo (1982). The case of the rainbow trout *Salmo gairdneri* Richardson is not clear. Kendall and Dale (1979) reported no microridges on secondary lamellae, whereas Olson and Fromm (1973) and Hughes (1979) reported them to be present. More species under different exposure regimes and fixation procedures need to be examined by SEM to determine the nature and possibly the functions of these structures. In heat-stressed rainbow trout, the loss of microridges on gill surfaces was attributed to increased mucus production filling the depressions between the microridges (Jacobs et al. 1981). Jagoe and Haines (1983) reported that microridges on gills of Sunapee trout *Salvelinus alpinus oquassa* dissappeared after exposure to pH 3 for 4 hours. They suggested that cellular swelling or membrane alterations were responsible. Cellular swelling generally occurs after acutely injured cells lose cell volume regulation (Trump and Ginn 1969). We consider the loss of microridges in fish exposed to space shuttle exhaust plume to be part of a spectrum of changes that probably eventually leads to necrosis. LM, TEM, and SEM did not reveal an excess of mucus among microridges of the fish we examined.

Fromm (1980) reviewed the effects of acid stress on freshwater fish and concluded that death may be caused by hypoxia brought on by alteration of gill membranes, coagulation of gill mucus, or a combination of the two. Gill mucus coagulation did not occur in the present study. However, mucus was apparently discharged in exposed fish. Daye and Garside (1976) found that stress by pH caused hypertrophy and stimulated mucus secretion in gills of brook trout *S. fontinalis.* We did not see hypertrophy of mucous cells, but the heterogeneity of secretory granules in intermediate and full exposure groups suggested to us that those cells had been stimulated to release their stored mucus granules and had begun replacing them.

Several hypotheses have been advanced to explain the role of mucus secretion as a protective response to acid stress. The benefit of mucus to the stressed fish might depend on the mucus being a barrier to ions and water, its being polyanionic and concentrating cations, or its specific binding of calcium, which is important for maintenance of permeability control (see review by McDonald 1983).

Damage to secondary lamellae must be considered potentially serious because of the possible effects on respiration. Hughes and Morgan (1973) reviewed the general histopathological responses of secondary lamellae to pollutants. An initial response is thickening of the gill epithelium due to swelling in acute exposures or to cell proliferation in long term exposures. Next, secondary lamellae fuse, the pavement cell layer lifts, and pavement cells dissociate. Epithelial lifting might help protect the gill from a toxicant

by increasing the diffusion distance between the ambient water and the fish's blood (Morgan and Tovell 1973) or by limiting water circulation between gill lamellae. In the present study, fusion of lamellae occurred not only between broad sheets of epithelium, but also processes of individual epithelial cells bridged the interlamellar space and joined adjacent lamellae. Using SEM, Engelhardt et al. (1981) reported fusion between broad areas of lamellae in rainbow trout exposed to crude oil emulsions whereas Jacobs et al. (1981) illustrated a focal type of fusion between secondary lamellae of heat-stressed rainbow trout. Possibly, the most severe gill injury that we saw in full exposures consisted of sloughing of epithelial cells of secondary lamellae, sometimes exposing the underlying capillary network. A similar effect was noted by Daye and Garside (1976) in secondary lamellae of rainbow trout exposed to environments at and above pH 9.0 and below 5.6.

Chloride cells, which are involved in monovalent ion regulation, occur in both euryhaline and stenohaline species of freshwater and marine fishes. These cells are located mainly in the interlamellar regions of filaments but in marine and seawater-adapted species also along the surface of the filament related to the afferent filament artery (Laurent and Dunel 1980). Hossler et al. (1979b) showed with SEM that the numerous pores on filament surfaces of seawater-adapted *M. cephalus* represented apical pits of chloride cells. In freshwater-adapted specimens, pores were shallower, and cytoplasm of chloride cells extended above the level of the pavement epithelium. We confirmed the identity of chloride cells by LM and TEM. With SEM, changes in the size, distribution or depths of filament pores after exposure could not be documented. Some filament pores, however, might represent evacuated mucous cells.

Tissue damage does not necessarily indicate the cause of a fish's death (Hughes and Morgan 1973). In heat-killed specimens of the banded killifish *Fundulus diaphanus* (Lesueur), Rombough and Garside (1977) considered the cause of death to be respiratory failure resulting from lesions in the medulla oblongata despite the presence of primary gill injury. For acutely lethal concentrations of some toxicants, however, death might not be accompanied by tissue damage. In gills of rainbow trout exposed for 2.5 h to lethal concentrations of ammonia, Smart (1976) reported neither increased mucus production nor hemorrhage. He concluded that gill damage was not the cause of death in that situation.

Whether fish surviving the acute exposure to the exhaust plume can recover is not known with certainty. The time course and mechanisms involved in repair of damaged tissues must be determined in controlled, laboratory experiments. Lloyd and Jordan (1964) found that rainbow trout that survived exposure to pH 3.8 for 24 h recovered when transferred to clean water. Recovery from the exhaust plume, however, is indicated by several factors. First, fish kills that are caused by the exhaust plume occur abruptly, and fish do not continue to die afterwards. Second, examination of fishes from the lagoon area that had been the site of previous kills revealed no latent pathologic changes that might have been related to previous exposures to the exhaust plume. However, lagoon fish might have been more susceptible to subsequent exhaust plume exposure since a much higher percentage of them died in full exposures than did fish from Molly Pond.

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PLATE 1

EXPLANATION OF FIGURES

1. *Cyprinodon variegatus* from control exposure. Filament (F); secondary lamellae (L). Paraffin section; hematoxylin and eosin stained. X 430.
2. *C. varigatus* from control exposure. Chloride cell (C); red blood cells (R). Epoxy resin section; toluidine blue stained. X 430.
3. *C. variegatus* from control exposure. Note chloride cell with central opening (*) probably representing apical pit. Mucous cells (M). Epoxy resin section; toluidine blue stained. X 430.
4. *C. variegatus* from control exposure. Secondary lamellae (L); filament (F). Scanning electron micrograph. X 370.
5. *C. variegatus* from control exposure. Pores (P) on filament surface are probably those of chloride cells. Note microridge patterns (arrowheads) that delineate individual pavement epithelial cells. Scanning electron micrograph. X 3,660.

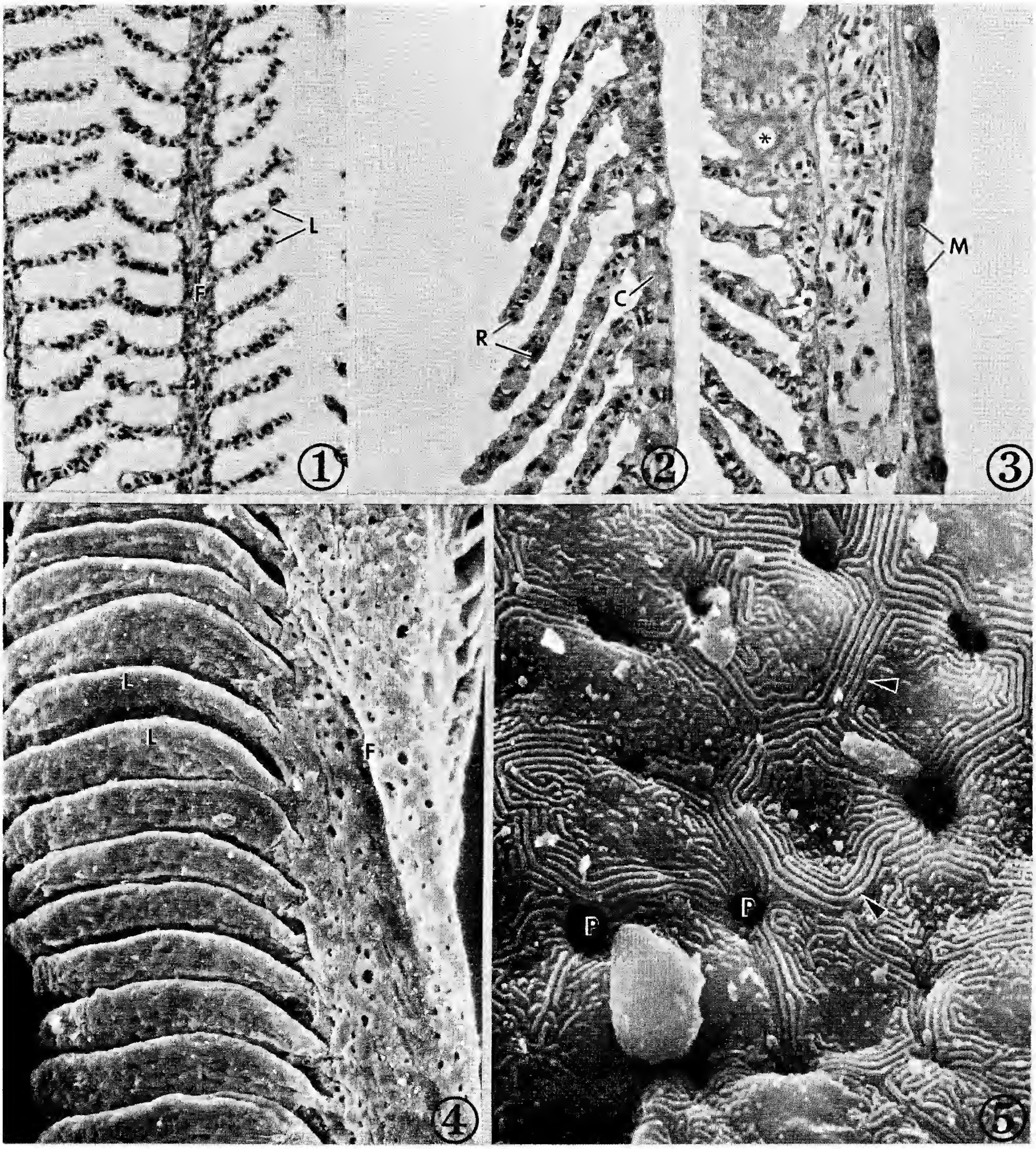

L
F
1
R
C
2
*
M
3
L
L
F
4
P
P
5

PLATE 2

EXPLANATION OF FIGURES

6. *Cyprinodon variegatus* from intermediate exposure. Note angulation of secondary lamellae and that the lamellae are somewhat thicker than control lamellae in Figures 1–3. Epoxy resin section; toluidine blue stained. X 430.

7. *C. variegatus* from intermediate exposure. Note shortening, wrinkling, and swelling of secondary lamellae. Also, mucous cells (M) have different densities. Filament cartilage (FC). Epoxy resin section; toluidine blue stained. X 430.

8. *C. variegatus* from intermediate exposure. Note mucous cells (arrowheads) on filament surface bulge outward slightly. Epoxy resin section; toluidine blue stained. X 430.

9. *C. variegatus* from intermediate exposure. Note depressions (*) in interlamellar regions of filament. Scanning electron micrograph. X 730.

10. Enlargement of filament surface shown in Figure 9. Note numerous bulging cells, probably mucous cells (M) and many pavement epithelial cells partially devoid of microridges (*). Chloride cell pore (P). X 1,830.

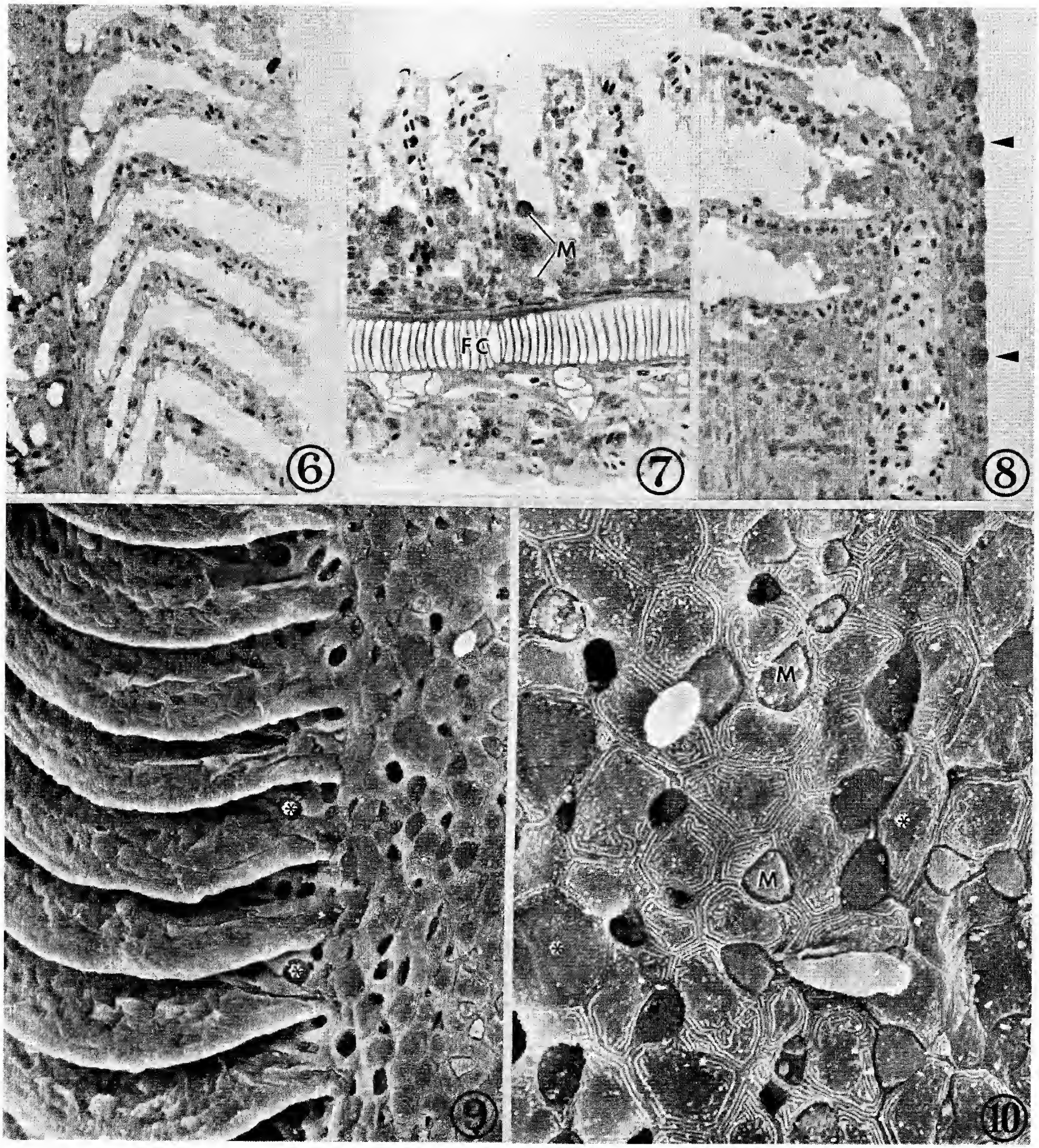

M
FC
6
7
8
M
M
9
10

PLATE 3

EXPLANATION OF FIGURES

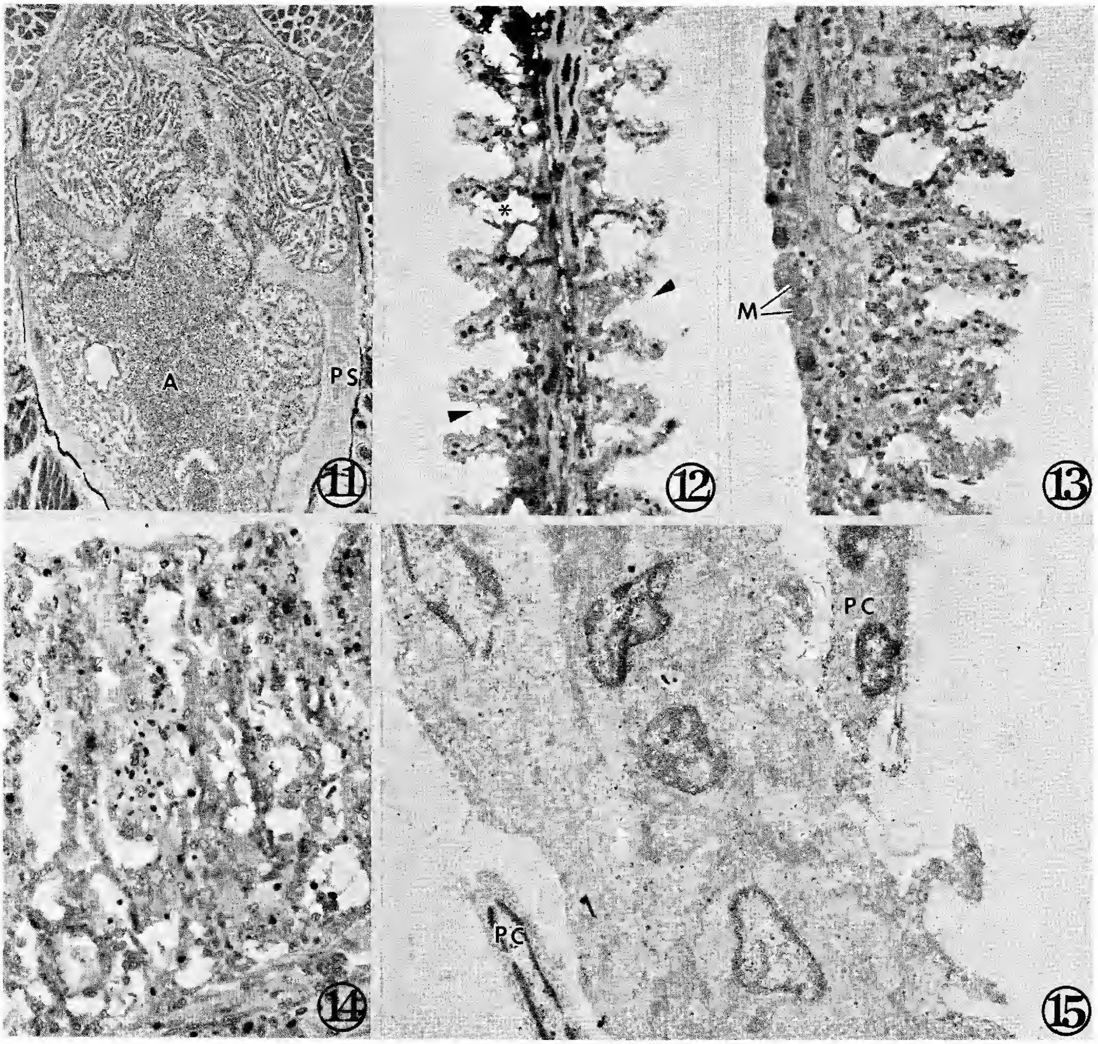
11. *Poecilia latipinna* that died from full exposure. Note blood congestion in atrium (A) of heart and transudate in pericardial space (PS). Paraffin section; hematoxylin and eosin stained. X 70.

12. *P. latipinna* from full exposure. Note retracted lamellae, wrinkling of pavement epithelial cells (arrowheads) and areas of epithelial lifting (*). Epoxy resin section; toluidine blue stained. X 430.

13. *P. latipinna* from full exposure. Note mucous cells (M) are lightly staining. Epoxy resin section; toluidine blue stained. X 430.

14. *Cyprinodon variegatus* that died from full exposure. Lamellae have fused so that normal architecture is disrupted. Epoxy resin section; toluidine blue stained. X 430.

15. *C. variegatus* that died from full exposure. Pavement epithelial cells (PC) are necrotic and separated from secondary lamella. Transmission electron micrograph. X 10,380.



A
PS
11
*
12
M
13
14
PC
PC
15

PLATE 4

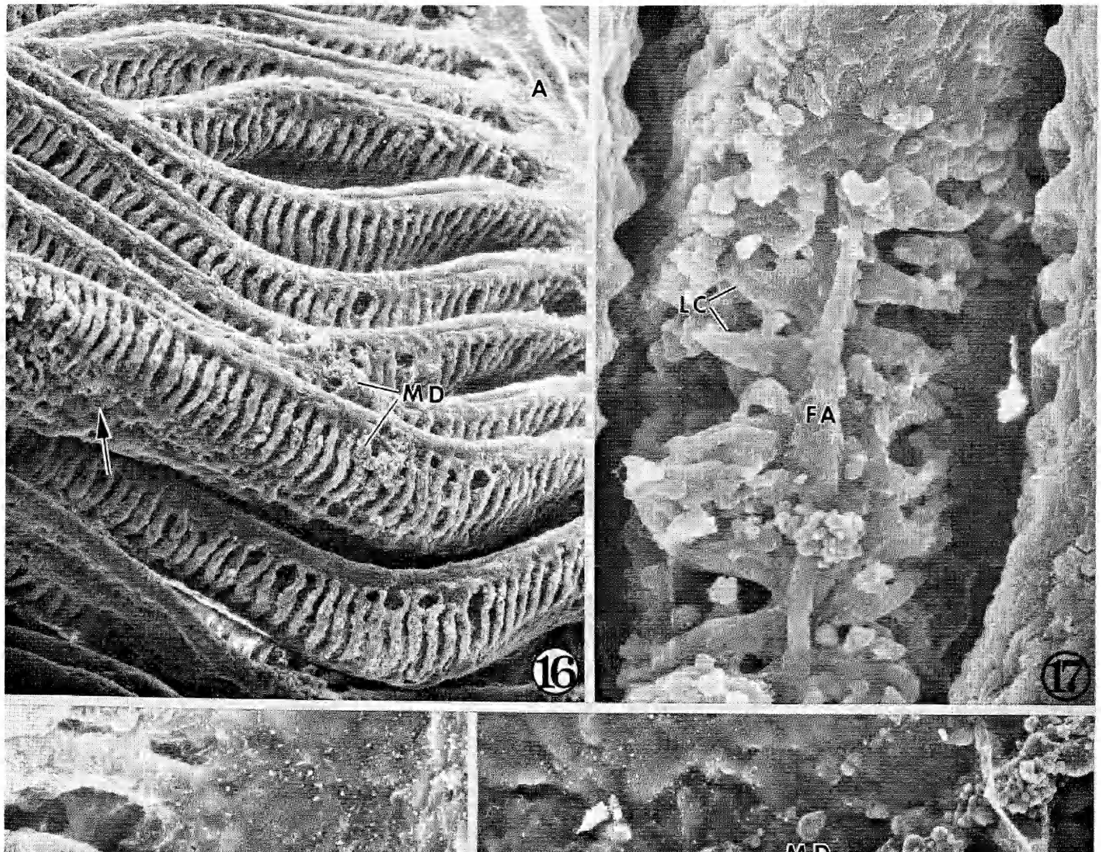
EXPLANATION OF FIGURES

16. *Poecilia latipinna* from full exposure. Note areas of damaged secondary lamellae (arrow). Gill arch (A); mineral deposits (MD). Scanning electron micrograph. X 210.

17. *P. latipinna* from full exposure. Loss of superficial epithelium reveals artery (FA) and lamellar capillaries (LC). Scanning electron micrograph. X 830.

18. *P. latipinna* from full exposure. Note absence of microridges from filament surface (F). Scanning electron micrograph. X 830.

19. *C. variegatus* that died from full exposure. Note fusion between broad areas of lamellae (*) and between narrow cellular bridges (arrows). Nuclei of pavement epithelial cells (arrowheads). Mineral deposits (MD). X 830.


A
MD
16
LC
FA
17
F
18
MD
*
19

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Distribution and Ecology of the Synaphobranchidae of the Gulf of Mexico

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DISTRIBUTION AND ECOLOGY OF THE SYNAPHOBRANCHIDAE OF THE GULF OF MEXICO

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ABSTRACT Synaphobranchid eels of the Gulf of Mexico are an important part of the upper continental slope ichthyofauna, occurring most frequently between 500 and 1,500 m. Two of the four known genera (*Histiobranchus* and *Diastobranchus*) have not been reported from the Gulf. Synaphobranchidae tend to occur within a narrow range of temperatures compared to the North Atlantic synaphobranchid eels. However, distribution of these eels in the deeper parts of the Gulf appears to be correlated more to change in depth than to temperature, salinity, or dissolved oxygen. The distribution at the shallower limits of their depth range appear to be a result of synergistic effects of the dissolved oxygen demand and the change in temperature. The synaphobranchid eels' apparent preferences for particular types of substrata are probably associated with the organisms preyed on rather than direct selection of bottom type by the eels. These eels are opportunistic feeders, feeding primarily on fish, squid, and crustaceans. Synaphobranchidae are frequently infested with parasites, but there do not appear to be any serious abnormal morphological results.

INTRODUCTION

Investigation of the deep-sea ichthyofauna has usually been conducted on a broad survey basis. Investigators have compiled lists and descriptions of families, genera, and species occurring throughout a particular area with a limited number of studies of the distributional and ecological aspects of individual groups of fishes. Springer and Bullis (1956) and Bullis and Thompson (1965) published a list of fishes collected in the Gulf of Mexico by the U.S. Fish and Wildlife Service research vessels which contained station locations, depths of capture, and for some stations, bottom type and temperature. Also, from these cruises Grey (1956, 1958, and 1959) published descriptions of the abyssal benthic fishes with short remarks about their general distribution and depths of capture. However, only a few investigations dealing with the distribution and ecology of particular families exist; most are lists (Mead 1952) or annotated checklists with some discussion of distribution and ecological factors included (Bright 1967). This investigation is particularly concerned with the eel group, about which ecological studies are practically nonexistent. Specifically, the purposes of this study are to describe the distribution and ecology of the family Synaphobranchidae for the Gulf of Mexico.

The paucity of information, until recently, on the distribution of synaphobranchid eels in the Gulf of Mexico and Caribbean Sea reflects the absence of intensive deep-sea exploration of this region. Synaphobranchid eels were first recorded in the Gulf of Mexico by Agassiz (1888) while working on the Blake collections. Adjacent to the Gulf, Parr (1932) working with collections from the PAWNEE expedition reported captures of *Ilyophis* and *Synaphobranchus* specimens from the Great Bahama Banks southeast of the Straits of Florida.

Castle (1960) described a new species of synaphobranchid eel, *Synaphobranchus oregoni,* from the Gulf and reported the occurrence of *Synaphobranchus brevidorsalis,* previously reported as *Synaphobranchus kaupi* by Grey (1956). In a doctoral dissertation on the deep-sea fish of the Gulf of Mexico, Bright (1967) noted the occurrence of several species of synaphobranchid eels with their distribution and some important ecological factors. Robins (1968) discussed some aspects of the distribution and general ecology of the family Synaphobranchidae in the Straits of Florida.

METHODS

Eel samples for this investigation were collected during cruises of the R/V ALAMINOS under the direction of Dr. Willis Pequegnat. Collections for this study were made with the benthic skimmer (Pequegnat, Bright, and James 1970), 2-m dredge, and the 20-m otter trawl. Table 1 is a summary of pertinent station information. Cruises of the R/V ALAMINOS are designated by a number and letter system. For example, in the series 71A1710 the first two digits refer to the year, the letter A is for ALAMINOS, the next two digits denote the number of the cruise, and the final two digits indicate the station number. On occasion, the station number will be followed by a letter which indicates more than one haul made at that station. Identification was accomplished by radiographing each specimen and counting vertebrae.

Hydrographic data (temperature, salinity, and dissolved oxygen) and sediment samples were collected at most stations; however, in some instances it was necessary to supplement the existing data with data collected during physical and geological cruises in the same area. The hydrographic data were taken approximately 1 meter from the bottom which is within the range of occurrence of the Synaphobranchidae.

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TABLE 1

Summary of station data. Indicates cruise, number of specimens, depth, equipment, location, and species taken at each station.

Station	Number of Species	Depth (m)	Equipment	Latitude N	Longitude W	Species
Cruise 68A7 July 25 – August 11						
12B	3	900	Skimmer	29°14.0′	86°59.7′	*S. oregoni*
13A	8	1060	Skimmer	29°03.0′	87°15.0′	*S. oregoni* (4) *I. brunneus* (4)
13D	1	1463	Skimmer	28°59.0′	87°23.3′	*S. oregoni*
15D	3	1097	Skimmer	29°10.3′	87°31.5′	*S. oregoni* (1) *I. brunneus* (2)
15H	11	914	Skimmer	29°10.5′	87°16.0′	*S. oregoni* (10) *I. brunneus* (1)
17B	1	900	Skimmer	29°09.5′	87°02.0′	*S. oregoni*
Cruise 68A13 November 12–21						
1	6	878	Skimmer	25°38.0′	96°07.3′	*S. oregoni*
3	1	714	2-m dredge	25°39.0′	96°11.0′	*S. oregoni*
4	1	512	Skimmer	25°38.4′	96°18.3′	*S. oregoni*
8	5	732	Skimmer	26°18.0′	96°08.0′	*S. oregoni*
12A	4	1060–1317	Skimmer	25°31.0′	95°51.0′	*S. oregoni*
14	1	969	2-m dredge	25°39.5′	95°49.5′	*S. oregoni*
15	1	659–860	Skimmer	27°34.5′	95°10.5′	*S. oregoni*
16	1	714	2-m dredge	27°37.0′	95°08.0′	*S. oregoni*
23	2	732	Skimmer	27°35.0′	95°23.0′	*S. oregoni*
26	1	1371–1435	Skimmer	27°00.3′	95°08.0′	*S. oregoni*
Cruise 69A11 August 5–27						
4	8	1005	Skimmer	27°24.9′	94°44.5′	*S. oregoni*
27	2	778	Skimmer	18°54.0′	94°58.8′	*S. oregoni* *I. brunneus*
69	1	1371	Skimmer	20°07.5′	96°10.5′	*S. oregoni*
75	1	1134	Skimmer	21°26.0′	96°48.5′	*S. oregoni*
78	8	677–732	Skimmer	21°30.0′	96°55.0′	*S. oregoni*
83	1	1236	Skimmer	21°35.0′	96°45.0′	*S. brevidorsalis*
86	4	969–1097	Skimmer	21°41.0′	96°51.0′	*S. oregoni*
Cruise 69A13 October 4–16						
44	19	752	20-m trawl	28°58.0′	88°28.0′	*S. oregoni*
Cruise 70A10 July 4–30						
9	8	1146	20-m trawl	18°57.0′	87°09.0′	*S. brevidorsalis*
16	1	833–878	20-m trawl	16°11.1′	84°48.0′	*S. affinis*
29	1	1146	20-m trawl	11°31.8′	74°24.5′	*I. brunneus*
40	4	622–659	20-m trawl	12°40.0′	72°00.0′	*S. oregoni*
51	7	1097	20-m trawl	17°17.1′	79°50.6′	*S. brevidorsalis*
Cruise 71A7 July 13–25						
9	8	906	20-m trawl	26°32.0′	96°07.0′	*S. oregoni* (7) *I. Brunneus* (1)
10	6	936	20-m trawl	26°32.9′	96°06.4′	*S. oregoni*
11	4	637	20-m trawl	26°32.3′	96°13.3′	*S. oregoni*
43	61	1005–1847	20-m trawl	27°27.8′	92°46.0′	*S. oregoni*
49	42	936	20-m trawl	27°26.0′	92°42.0′	*S. oregoni* (41) *I. brunneus* (1)
57	10	1216–1234	20-m trawl	26°55.8′	92°57.9′	*S. oregoni*
Cruise 71A8 July 29–August 15						
24	12	659–695	20-m trawl	23°56.8′	97°05.0′	*S. oregoni*
29	34	936	20-m trawl	23°54.7′	96°59.9′	*S. oregoni*
36	2	2151	20-m trawl	23°35.6′	96°25.5′	*S. brevidorsalis*
47	35	936	20-m trawl	21°35.6′	96°54.6′	*S. oregoni*
60	77	1097–1134	20-m trawl	19°00.3′	95°11.1′	*S. oregoni*

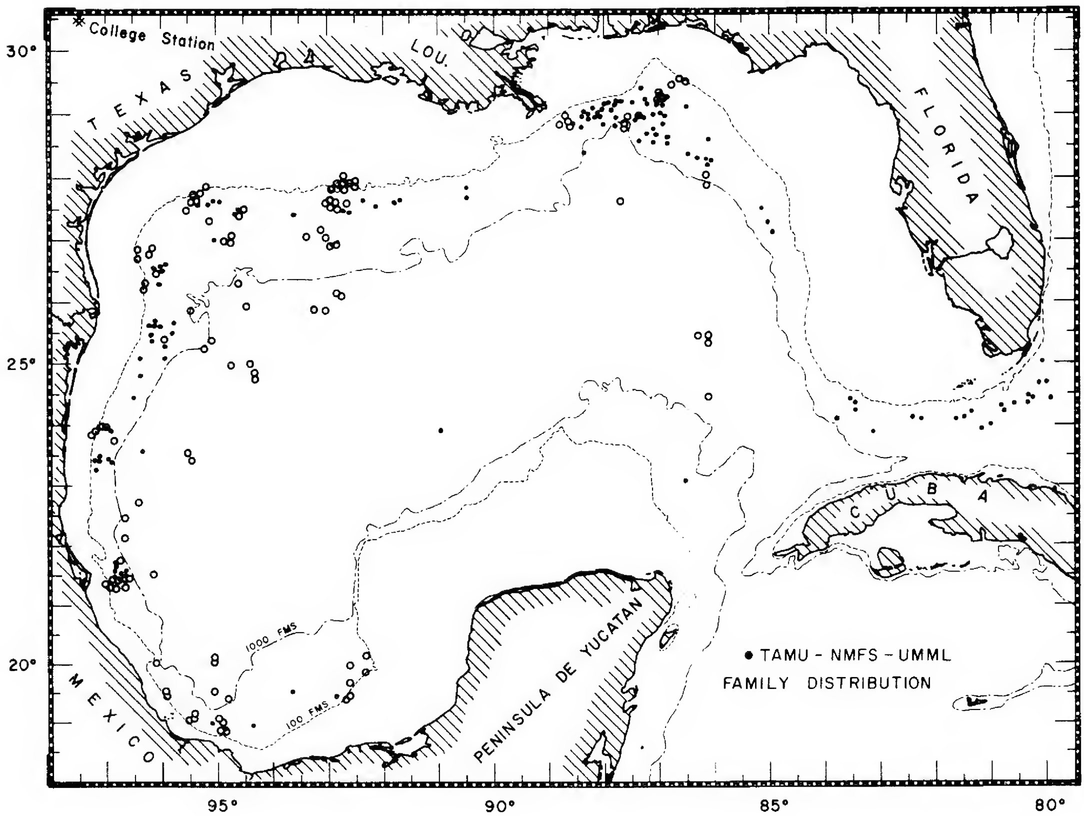

Figure 1. Distribution of the family Synaphobranchidae in the Gulf of Mexico. Data are derived from the collections of NMFS, UMML, and TAMU. The open circles show stations made by TAMU where no synaphobranchid eels were collected.

Sediment samples were collected with piston and gravity corers. Sediment size analyses were performed on the upper surface of the piston core samples for percent sand, silt, and clay. The upper surfaces of gravity cores were analyzed for percent sand and the remaining core fractions were analyzed for percent silt and clay combined.

DISTRIBUTION

Synaphobranchidae occur within a narrow depth range primarily around the northern, western, and southeastern areas of the Gulf of Mexico, which was determined from the collections of the University of Miami Marine Laboratory (UMML), the National Marine Fisheries Service (NMFS), and Texas A&M University (TAMU) (Figure 1). The open circles indicate trawl stations and benthic skimmer stations made by the R/V ALAMINOS where no synaphobranchid eels occurred. Limited sampling of the Yucatan Peninsula prevents any inference concerning the absence of synaphobranchid eels from that area. For the purpose of this investigation, the Gulf of Mexico was considered to extend no further than 80° west longitude. Therefore, a number of occurrences of synaphobranchid eels reported by Robins (1968) from the Straits of Florida do not appear on the distributional maps.

Between 1968 and 1971, 133 benthic stations were made by TAMU in the Gulf, 99 were taken with the benthic skimmer and 2-m dredge (modified skimmer). The remaining 34 stations were made with a 20-m otter trawl which was the most successful piece of sampling gear for taking demersal fishes. Of the skimmer stations, 25 contained 76 specimens of synaphobranchid eels. But from the 34 trawl stations, 11 contained 322 specimens representing approximately 78% of the collection.

The depth distribution of bottom stations made in the Gulf by TAMU, and the number of stations within a particular depth interval which contained synaphobranchid eels are presented in Table 2. An estimate of the probability of taking a species of the family Synaphobranchidae within a given depth range is included, together with the 95% confidence limits.

Depth distribution and total number of each species taken within a particular depth interval are shown in Table 3 and establish the depth range of each species. The depth ranges in the upper 1,500 m are considered closely representative of the actual distributions for these species. Below this depth, sampling is too sparse to make any conjectures as to the vertical limits of occurrence for the deeper dwelling members of the family. An examination of Tables 2 and 3 suggests that the synaphobranchid eels are primarily situated on the upper part of the continental slope between 500 and 1,500 m, with only one species occurring below 2,000 m.

TABLE 2

Depth distribution of bottom stations in the Gulf by TAMU (sample size) with number of stations containing synaphobranchid eels (occurrences), and the probability of occurrence of a species of the family in a particular depth interval with the associated confidence limit.

Depth (m)	Sample Size (n)	Occurrence (r)	Probability of Occurrence ($p=\frac{r}{n}$)	Confidence Limits (95%)
100–600	40	1	.02	.00–.05
600–1100	40	1	.63	.48–.78
1100–1600	23	8	.35	.15–.54
1600	30	1	.03	.00–.01

CONFIDENCE LIMITS = $p \pm 1.96\sqrt{\frac{p(1-p)}{n}}$ (R. V. Hogg and E. A. Tanis 1977).

TABLE 3

General depth distribution of synaphobranchid eels collected in the Gulf by UMML, NMFS, and TAMU. The values in each column represent the combined number of that species taken within the corresponding depth interval.

Depth (m)	*S. oregoni*	*S. brevidorsalis*	*S. affinis*	*I. brunneus*
100–199				
200–299				
300–399				
400–499				
500–599	1			
600–699	27		1	
700–799	57		9	6
800–899	22		12	1
900–999	152		2	7
1000–1099	84		1	6
1100–1199	77			1
1200–1299	12			
1300–1399	3	1		
1400–1499	1			
1500–1599				
1600–1699				
1700–1799				
1800–1899				
1900–1999				
2000–2099				
2100–2199		5		
2200–2299				

The family Synaphobranchidae contains four genera and eight species (Castle 1964), but only two genera and five species are recorded from the Gulf of Mexico. These are *Synaphobranchus oregoni* Castle, *S. brevidorsalis* Gunther, *S. affinis* Gunther, *S. kaupi* Johnson, and *Ilyophis brunneus* Gilbert. The two genera not represented are *Histiobranchus* and *Diastobranchus*. *Synaphobranchus kaupi* was not collected at any TAMU stations. The only occurrences recorded were taken by NMFS. Identification of these specimens was made in the field (Richard Roe, personal communication) and these could have been *S. affinis*, since the two species have a very similar scale pattern (Castle 1964). A histogram showing the frequency of distribution with depth for each species is presented in Figure 2 (a-d) and the horizontal distribution for each species is shown in Figure 3.

Synaphobranchus oregoni Castle, 1960

Vertical Distribution

The vertical range of *S. oregoni*, the most frequently occurring species collected by TAMU, is between 500 and 1,500 m (Figure 2a) placing this species in the upper continental slope fauna. Most specimens were collected between

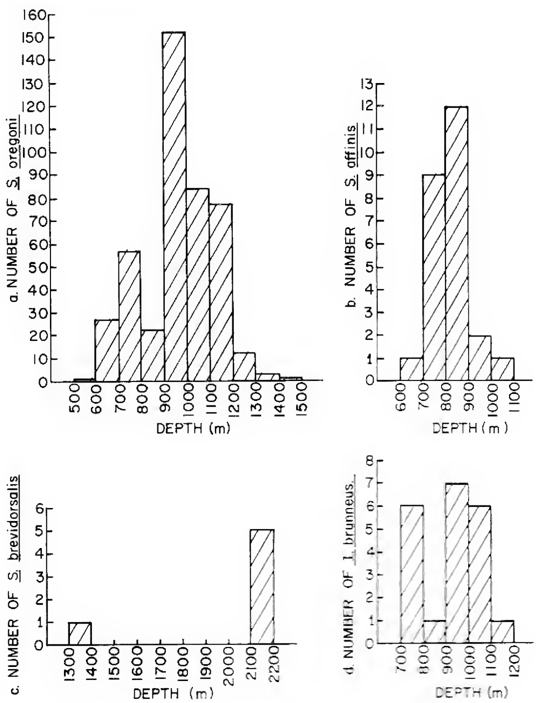

Figure 2 a-d. Frequency distribution with depth for *S. oregoni* (a), *S. affinis* (b), *S. brevidorsalis* (c), and *I. brunneus* (d).

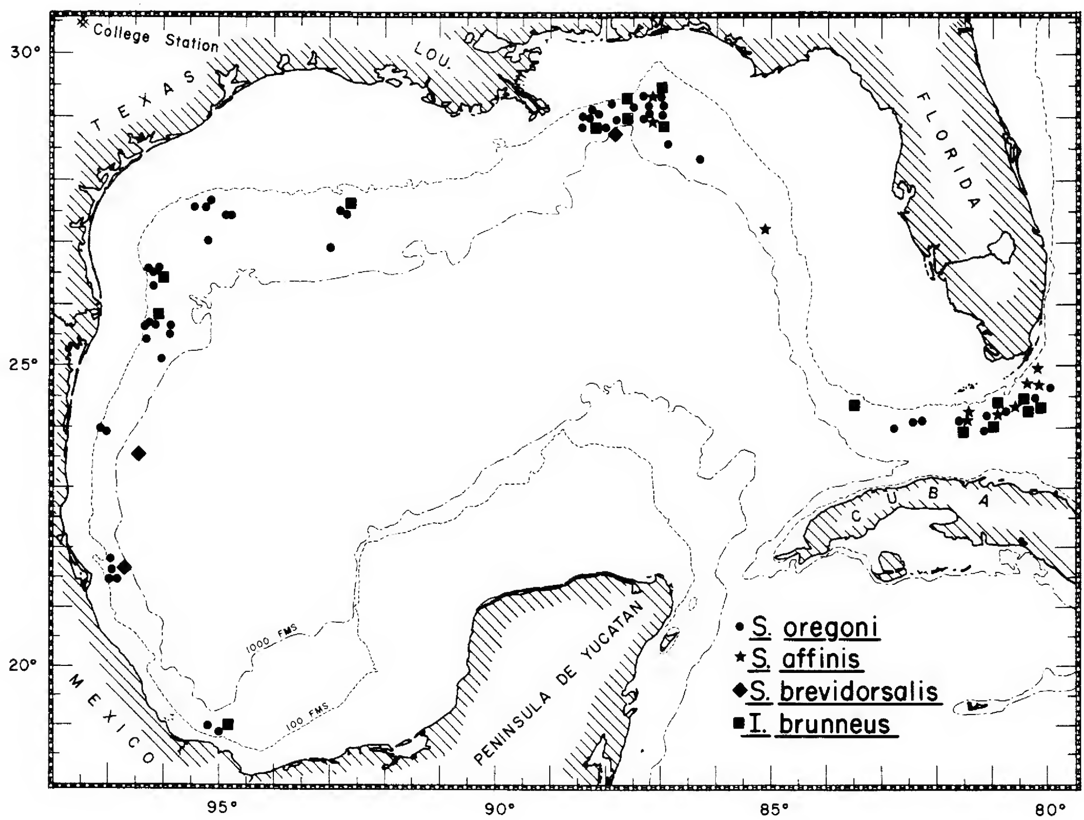

Figure 3. Horizontal distribution of *S. oregoni*, *S. affinis*, *S. brevidorsalis*, and *I. brunneus*.

900 and 1,000 m. The shallowest and deepest occurring specimens were recorded from the western Gulf at 512 m and 1,463 m, respectively. When comparing depths of maximum occurrence of *S. oregoni* from the western Gulf (936 to 1,134 m) with those reported by Robins (1968) from the Straits of Florida (750 to 823 m), there is a significantly wider and deeper range of occurrence for this species in the western Gulf. There does not appear to be any significant change in the depth of maximum occurrence in populations from north to south in the western Gulf based on the data from TAMU collections (Table 1).

Horizontal Distribution

Figure 3 shows the horizontal distribution of *S. oregoni* and indicates its occurrence throughout the Gulf. The absence of synaphobranchid eels off Yucatan was considered previously.

Robins (1968) reports a northern limit (Lat. 24°51′N) for *S. oregoni* in the Straits of Florida. From the data available for this investigation, the northern limit of *S. oregoni* for the Gulf proper is considered to be Lat. 29°18′N. However, there is an area farther north within the depth range of this species that has not been sampled by TAMU, but has been sampled extensively by the NMFS at Pascagoula, Mississippi (unpublished cruise report). It appears that the absence of *S. oregoni* in this area is due to limiting environmental factors which will be discussed in the Ecology Section. The apparent southernmost occurrence for *S. oregoni* in the Gulf of Mexico is Lat. 18°54′N. However, this is possibly due to insufficient sampling and may not be related to physical conditions.

Synaphobranchus affinis Gunther, 1877

Vertical Distribution

Synaphobranchus affinis was not collected at any of the TAMU stations. Therefore, the following discussion is based primarily on Robins (1968) and a species list supplied by the NMFS at Pascagoula, Mississippi. A large number of the specimens reported by Robins are not included here since

most were collected east of Long. 80°00′W, and, for the purpose of this study, are considered to be outside the Gulf of Mexico proper.

The vertical range of *S. affinis* for the Gulf is between 600 and 1,000 m, with the largest number being collected from the 800 to 900 m depth interval (Figure 2b). From Robins' (1968) data for the Gulf, the shallowest and deepest depths of occurrence for the species were reported at 671 m and 1,015 m, respectively.

Horizontal Distribution

The most significant aspects of the distribution of this species is its apparent absence from the western Gulf (Figure 3). Robins (1968) reported that *S. affinis* occurred most frequently north of Lat. 25°00′N, the largest concentration being found in the Straits of Florida. The most northern and western stations where *S. affinis* have been taken are Lat. 29°17′N and Long. 87°09′W, respectively. Figure 1 indicates the extensive sampling carried out in the western Gulf. Such extensive sampling without capture makes it highly probable that *Synaphobranchus affinis* is limited to the eastern section of the Gulf of Mexico.

Synaphobranchus brevidorsalis Gunther, 1887

Vertical Distribution

Figure 2c shows the vertical range of *S. brevidorsalis* to be approximately 1,300 to 2,200 m. The largest number of specimens occurred within the 2,100 to 2,200 m depth interval. Shallowest occurrence was at 1,326 m and the deepest was 2,151 m. Absence of *S. brevidorsalis* captures between 1,326 and 2,151 m is peculiar, and is not due to the lack of sampling. Table 2 shows extensive sampling over that depth interval. It is possible that this shallow specimen was *S. oregoni* with a reduced vertebral count or a migrant *S. brevidorsalis* from the Caribbean.

Horizontal Distribution

This species of synaphobranchid eel, although widespread, has not been collected in abundance from the Gulf of Mexico. At the present, only six specimens have been reported, three taken by the NMFS from the northeastern section, and three collected from the southwestern section by TAMU.

Figure 3 shows the locations where *S. brevidorsalis* have been collected. The small size of the population and wide horizontal distribution of this species is apparent when comparing the number of stations (3) containing *S. brevidorsalis* with the number of stations (33) containing other synaphobranchid eels.

The occurrence of *S. brevidorsalis* in the Gulf of Mexico presents an interesting distributional problem. Heretofore, this species had been reported from the Gulf of Mexico and the Indian and Pacific Oceans (Bruun 1937 and Grey 1956). Robins (1968), working with a large collection of synaphobranchid eels did not report any *S. brevidorsalis* from the Straits of Florida.

Two samples containing 15 specimens were taken in the Caribbean by TAMU in 1970. One station at 1,097 m contained seven specimens and the other from 1,146 m had eight. More extensive sampling is needed off the northeastern coast of South America to further elucidate the distribution of *Synaphobranchus brevidorsalis*.

Ilyophis brunneus Gilbert, 1891

Vertical Distribution

Ilyophis brunneus was the second most frequently occurring synaphobranchid eel, although it was generally not collected in large numbers (the most taken in any trawl was four). Usually, *I. brunneus* was captured singly or in pairs; perhaps this is due to the eel's burrowing habits.

Figure 2d shows the vertical range of *Ilyophis brunneus* to be 700 to 1,200 m with the maximum number of specimens collected from 900 to 1,100 m. A second peak (700 to 800 m) in the frequency distribution histogram implies that *I. brunneus* possibly occurs in equal numbers throughout its vertical range. Robins (Figure 33, 1968) also shows a maximum occurrence within the 700 to 800 m depth interval for *I. brunneus* in the Straits of Florida; however, the data do not indicate a second area of maximum occurrence within the 900 to 1,100 m depth interval. This could indicate that there are factors affecting the vertical distribution of this species in the Straits of Florida which are not found at those depths in the Gulf proper.

Horizontal Distribution

Figure 3 shows that *I. brunneus* is distributed throughout the Gulf, being collected from every major geographic section. *Ilyophis brunneus* appears to occur more frequently in the eastern and northern sections. This is indicated by a comparison of the number of captures with the number of trawl stations within each major geographic section (Table 1).

ECOLOGY

Ecological investigations of deep-sea fishes for the Gulf are few and ecological studies for deep-sea eels are nonexistent. One of the purposes of this study is to document the physical habitat and to some extent, the niche that the synaphobranchid eels occupy in the Gulf of Mexico. For the purpose of discussion, the ecology section is divided into two parts: (1) physical parameters where the temperature, salinity, dissolved oxygen, and sediment data are reported for each species, and (2) biological parameters where feeding habits and parasites are discussed.

Hydrographic data (Table 4) and sediment data (Table 5) were taken in the vicinity of, and on the same cruises as, the trawl stations where synaphobranchid eels were collected. Close proximity of these hydrographic, sediment, and

TABLE 4

Hydrographic Data

Station	Lat. (N)	Long. (W)	Depth (m)	T (C)	S (ppt)	0_2 (ml/l)
71A7-25	27°54.6′	92°49.9′	209	13.95	35.783	2.608
71A7-21H	26°43.6′	96°25.5′	227	12.98	35.597	2.425
67A5-13C	29°30.0′	86°52.5′	350	10.75	35.305	2.835
71A7-36	27°36.5′	92°58.4′	460	8.84	35.076	2.536
71A8-69	19°39.3′	92°40.8′	536	7.69	34.988	2.658
71A8-45	21°25.5′	96°55.8′	547	7.56	34.928	2.631
71A8-5H	26°38.0′	96°15.0′	582	7.32	34.879	2.794
67A5-9B	29°27.0′	86°51.1′	676	6.62	34.883	3.104
67A5-6F	28°47.3′	87°02.8′	750	5.73	34.885	3.511
66A5-5	27°52.5′	90°22.0′	785	5.77	34.895	3.450
65A3-1	27°30.0′	95°30.0′	813	5.52	34.899	3.870
67A5-7G	29°15.5′	86°59.0′	867	5.32	34.902	3.735
71A8-28	23°56.1′	97°01.3′	903	5.03	34.941	3.886
71A7-44	27°30.4′	92°49.3′	924	5.09	34.914	3.781
69A11-6	27°25.0′	94°45.6′	937	4.88	34.936	3.923
71A7-8H	26°31.2′	96°05.5′	957	5.02	34.876	3.861
71A8-62	19°01.0′	95°11.0′	1034	4.75	34.945	4.046
68A3-15B	26°28.8′	95°59.0′	1086	4.52	34.948	4.515
71A7-59	26°59.1′	92°58.5′	1193	4.38	–	4.429
71A8-77	20°06.8′	92°20.4′	1316	4.28	34.964	4.638
71A8-53	21°37.1′	96°09.7′	1818	4.22	34.936	4.819
71A8-9	26°07.5′	92°42.0′	2043	4.20	34.987	4.813
71A8-35	23°39.0′	96°26.5′	2123	4.23	34.980	4.834
71A8-39	23°28.3′	95°30.3′	3006	–	34.981	4.936
69A13-34	26°50.5′	86°40.0′	3074	4.32	34.780	5.024
66A5-3	25°25.0′	86°13.0′	3204	4.28	34.974	5.090
69A13-31	25°26.0′	86°09.0′	3221	4.33	34.876	4.990
68A7-4C	25°25.3′	86°05.3′	3246	4.32	35.143	5.388
71A8-15	25°05.8′	94°23.1′	3665	4.42	34.972	4.804

trawl stations presents an opportunity to compare the occurrence of some species of synaphobranchid eels with, essentially, direct observations of the environmental parameters. The hydrographic data were collected during spring, summer, and fall cruises and show little variation seasonally at the depths occupied by synaphobranchids. To further show the uniform nature of the bottom temperature, salinity, and dissolved oxygen along the slope, data from Table 4 were plotted in Figure 4 (A–C) on a hydrographic transect (solid line) across the northern slope between 26° to 28° north latitude and 92° to 93° west longitude. The close fit of the data to the profiles of the transect indicate uniform conditions horizontally and are considered to be representative of the condition under which the eels generally occur.

PHYSICAL PARAMETERS

Temperature

A discussion of temperature effect on animal distribution and behavior was presented by Gunter (1957), where he considered the magnitude of change of the temperature to be of major importance. Table 4 shows that the temperature decreased with increasing depth to about 2,000 m, where it reached a minimum of 4.20°C and then increased to 4.42°C due to adiabatic heating. Figure 4A is a transect of bottom temperatures (solid line) across the northern slope. It is clear from the slope of the temperature profile that the variability of the temperature range also decreased with increasing depth to approximately 1,300 m. The temperature varies by less than 0.10°C between 1,300 and 2,000 m.

Synaphobranchus oregoni. There was a gradual decrease in the bottom temperatures with depth through the 500 to 1,500 m vertical range of *S. oregoni*. The temperature ranged from 7.70°C to 4.24°C over this depth interval (Figure 4A), representing a temperature difference of 3.46°C. The largest number of specimens occurred within the 900 to 1,000 m range with a corresponding temperature range of 5.20°C to 4.75°C or a variation of 0.45°C. *Synaphobranchus oregoni* tended to occur most frequently at depths where the temperature begins to vary the least. This is illustrated in Figure 2a, where the frequency of distribution is shown to be skewed toward the deeper depths with the least variable temperature. Table 2 also shows that the probability of capturing *S. oregoni* below 600 to 1,100 m was higher than above that depth interval. The equal number of attempts within each interval indicated

TABLE 5

Sediment Data

Station	Lat. (N)	Long. (W)	Depth (m)	Sand (%)	Silt (%)	Clay (%)	Silt-Clay (%)
68A3-11C	26°18.5′	96°22.0′	91	89.4			10.6
71A8-42	21°21.7′	97°01.5′	179	0.9			99.1
67A5-11B	29°25.0′	86°20.0′	190	26.8			73.2
67A5-13D	29°30.0′	86°52.0′	379	28.1			71.9
71A8-68	19°39.3′	92°40.8′	528	2.7			97.3
71A8-44	21°25.3′	96°55.8′	565	2.0			98.0
70A8-8	29°17.5′	87°09.0′	686	2.7	14.5	82.8	97.3
68A3-12B	26°21.0′	96°08.5′	752	3.0			97.0
71A8-28	23°56.1′	97°01.3′	900	1.3			98.7
67A5-7B	29°08.0′	87°09.5′	918	13.2			86.8
68A3-14B	26°25.0′	96°03.8′	955	2.7			97.3
71A8-61	19°00.0′	95°11.0′	1057	3.4			96.6
68A3-15C	26°28.8′	95°59.0′	1104	1.6			98.4
71A7-60	26°57.4′	92°58.5′	1216	9.3			90.7
70A8-11	28°30.7′	87°20.6′	1335	2.9	16.7	80.4	97.1
71A8-76	20°06.4′	92°19.2′	1337	4.3			95.7
70A8-34	26°43.2′	93°38.2′	1348	6.9	14.5	78.6	93.1
67A5-5	28°27.2′	87°20.0′	1476	8.4			91.6
70A8-12	27°32.1′	85°23.1′	1646	20.2	30.0	49.8	79.8
70A8-9	29°00.8′	87°29.3′	1650	1.5	12.3	86.2	98.5
70A8-33	26°45.2′	94°10.6′	1716	1.7	16.9	81.4	98.3
70A8-32	26°39.0′	94°44.0′	1778	5.0	13.8	81.2	95.0
71A8-7	26°07.0′	92°56.0′	2113	12.9			87.1
70A8-10	28°43.2′	87°45.5′	2158	3.8	13.5	82.7	96.2
68A3-3D	25°09.0′	94°11.0′	3658	2.2			97.8

that the probabilities were not greatly biased by sample size, and since all trawls were fished about 30 minutes, approximately the same amount of bottom was covered for each station.

The maximum and minimum temperatures recorded within the range of distribution of *S. oregoni* in the Gulf of Mexico were 7.70°C and 4.24°C, respectively. As noted above, a minimum temperature of 4.20°C. occurred at approximately 2,000 m and beyond that depth the temperature increased to 4.42°C as a result of pressure. These data show only a 0.04°C change in temperature from 1,500 to 2,000 m, which indicates that either these eels were unable to adapt to the temperature differential for physiological reasons at 2,000 m depth (at which the ambient temperature beings to increase), or that some other limiting factors (such as sediment type or pressure) were involved in restricting *S. oregoni* from inhabiting the lower continental slope or rise.

Synaphobranchus affinis. The temperature ranged from 6.30°C to 4.70°C over the depth interval 600 to 1,000 m from which *S. affinis* was collected (Figure 4A). *Synaphobranchus affinis* was reported most frequently from 800 to 900 m where the temperature ranged from 5.90°C to 5.20°C. Temperature varied by 1.60°C over the 400 m depth span from which *S. affinis* was collected and by 0.70°C over the depth interval from which this species was most frequently reported.

Synaphobranchus brevidorsalis. The temperature range over the depth interval 1,300 to 2,200 m from which *S. brevidorsalis* was reported was 4.30°C to 4.12°C (Figure 4A), a variation of 0.18°C. Although this species of synaphobranchid had a wide vertical distribution, it occurred at depths where temperature varied at most by 0.10°C and was most frequently collected at depths where the temperature varied by less than 0.03°C.

Ilyophis brunneus. The temperature range for *I. brunneus* was 6.50°C to 4.50°C, based on the vertical range established in Figure 2d. *Ilyophis brunneus* was collected most frequently between 900 and 1,100 m, which had a temperature range of 5.20°C to 4.50°C (Figure 4A); and in almost equal numbers from the 700 to 800 m depth interval, which had a temperature range of 6.50°C to 5.90°C.

Salinity

There are few reports relating salinity to distribution of deep-sea fishes in the Gulf of Mexico. Although salinity is considered a rather stable factor in the deep waters of the Gulf, Ichiye and Sudo (1971) have shown that long-term secular variations of a few hundredths of a ppt over 5-year periods do occur within the depth range of the Synaphobranchidae. Another interesting feature of the vertical distribution of salinity is the presence of high-salinity water (over 35.000 ppt) which flows westward along the southern

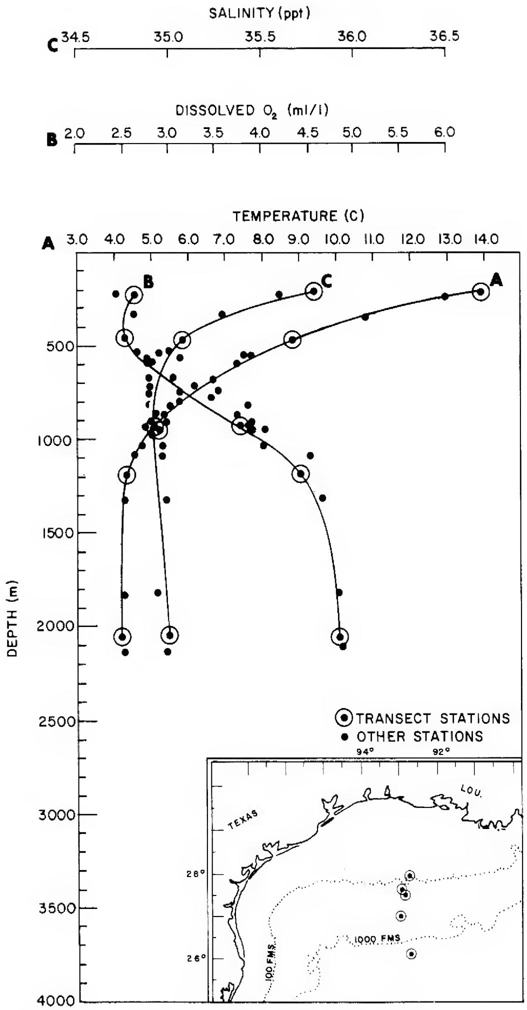

Figure 4 A–C. Transect of hydrographic data (solid line) from the northern continental slope of the Gulf of Mexico.

continental slope and northward along the western slope (Ichiye and Sudo 1971).

A salinity profile indicates a general trend of decreasing bottom salinity with increasing depth to about 900 m where the salinity begins to increase with depth (Table 4). When bottom salinities from other stations in the Gulf are plotted on the northern slope transect, a slightly variable structure of salinity (horizontally) is evident.

Synaphobranchus oregoni. The salinity between 500 and 1,500 m decreases from 34.99 ppt at 536 m to 34.88 ppt at 957 m where the salinity then begins to increase to approximately 34.90 ppt at 1,500 m (Table 4). The salinity is slightly more variable horizontally at 500 m (approximately 0.14 ppt) than it is at the deeper depths (approximately 0.04 ppt). *Synaphobranchus oregoni* was most frequently collected within 900 to 1,000 m where the salinity range was typically 34.94 to 34.91 ppt and could be expected to vary by about 0.04 ppt horizontally.

Synaphobranchus affinis. The salinity range for *S. affinis* is from 35.00 to 34.88 ppt (Figure 4C) based on the vertical range established in Figure 2b. *Synaphobranchus affinis* was most frequently collected from 800 to 900 m, which had a salinity range of 34.93 to 34.91 ppt with expected horizontal variations of up to 0.02 ppt.

Synaphobranchus brevidorsalis. Salinity within the 1,300 to 2,200 m depth interval increases slightly from 34.96 to 34.98 ppt which indicates a salinity change of less than 0.02 ppt. *Synaphobranchus brevidorsalis* was reported most frequently from 2,100 to 2,200 m where salinities were typically 34.98 ppt and is shown (Table 4) to vary by less than 0.01 ppt from 2,000 to 3,000 m.

Ilyophis brunneus. Within the 700 to 1,200 m depth interval from which *I. brunneus* was reported, the salinity (Table 4) decreases from 34.96 to 34.88 ppt at 957 m and then increases to 34.92 ppt at 1,200 m. *Ilyophis brunneus* was most frequently collected from 900 to 1,100 m and the salinity ranged from 34.92 to 34.91 ppt and varied horizontally by approximately 0.02 ppt (Figure 4C).

Dissolved Oxygen

The distribution of dissolved oxygen differs from that of the conservative properties of sea water (temperature, salinity, etc.), since oxygen concentration is affected by biological and chemical processes. Richards (1957) discussed at length the processes which affect the distribution of dissolved oxygen in the oceans and various concepts on the origin of the oxygen minimum zone.

The oxygen-minimum layer (2.50 ml/l) for the Gulf of Mexico has been described by Nowlin (1971) and occurs at approximately 300 m in the western Gulf, 600 m in the eastern Gulf, and 700 m near the Yucatan Straits. There is a secondary oxygen-minimum layer (3.50 ml/l) which occurs at approximately 250 m in the eastern Gulf and Yucatan Straits.

Bruun (1957) stated that a correlation between concentration of dissolved oxygen and distribution of organisms may be expected, but it is not possible to demonstrate. There does not appear to be any conclusive evidence in the literature that dissolved oxygen concentration in the deep sea is low enough to have a direct effect on the distribution of deep-sea organisms by putting them under pysiological stress. Oxygen levels may in some cases be indicators of reduced concentrations of other nutrient elements which have a limiting effect on the occurrence of organisms, such as the concentration of phosphate and nitrate, which is inversely proportional to the oxygen concentration (Richards 1957).

Figure 4B shows a profile of bottom oxygen concentrations for a transect of hydrographic stations from the northern slope of the Gulf of Mexico. The dissolved oxygen concentration increases rather rapidly with increasing depth from 500 to 1,200 m. Below 1,200 m, oxygen continues to increase but more slowly. Other important features of the oxygen profile which should be noted are the occurrence of the oxygen-minimum layer between 200 and 400 m and the variable nature of the oxygen concentration levels below 3,000 m. These two features, however, do not occur within the reported depth range of the Synaphobranchidae.

Synaphobranchus oregoni. The dissolved oxygen concentration increased from 2.66 to 4.64 ml/l (Figure 4B), a change of 1.98 ml/l within the 500 to 1,500 m depth interval. Most of the *S. oregoni* specimens were collected from 900 to 1,000 m where oxygen levels range from 3.89 to 4.05 ml/l, a 0.16 ml/l range. Based on the oxygen distribution shown in Figure 4C and the oxygen range established for *S. oregoni* with this investigation, it was apparent that the dissolved oxygen concentration was not a major factor influencing the distribution of *S. oregoni* to deeper parts of the slope. Oxygen could, however, be an important factor limiting the distribution of *S. oregoni* into shallower depths. A gradual increase in the depth of the oxygen-minimum layer from west to east coincides with the reported minimum depths of occurrence of *S. oregoni.* Robins (1968) reported an upper limit of 679 m for *S. oregoni* in the Straits of Florida, where the oxygen-minimum layer is around 600 m.

Synaphobranchus affinis. The dissolved oxygen concentration increased from 2.79 to 4.32 ml/l (Figure 4B) over the reported vertical range of 600 to 1,100 m for *S. affinis* as shown in Figure 2b. This represented a 1.53 ml/l change in oxygen concentration over the depth of occurrence. *Synaphobranchus affinis* was reported most frequently from the 3.38 to 3.89 ml/l oxygen range which indicated a 0.51 ml/l change in oxygen within the 800 to 900 m depth interval. Dissolved oxygen may have a similar limiting influence on the vertical distribution of *S. affinis* as that described for *S. oregoni.*

Synaphobranchus brevidorsalis. The dissolved oxygen concentration increased slightly from 4.64 to 4.83 ml/l (Figure 4B) within the reported vertical range (1,300 to 2,200 m) of *S. brevidorsalis,* which represented a 0.20 ml/l range in oxygen concentration.

The oxygen concentration changes by 0.20 ml/l over the 1,300 to 2,200 m depth interval reported for *S. brevidorsalis* and this eel was most frequently collected within the 2,100 to 2,200 m depth interval, where the dissolved oxygen concentration is shown to change very little both vertically and horizontally (Figure 4C). At 1,300 m the slope of the oxygen profile begins to change rather rapidly with decreasing depth. The oxygen concentration decreased by about 35% within approximately 200 m (1,300 to 1,100 m), which represents a substantial change to an animal whose environment is constantly at a low temperature and a high oxygen content.

Ilyophis brunneus. The dissolved oxygen concentration increased from 3.10 to 4.43 ml/l (Figure 4B) over the 700 to 1,200 m depth interval from which *Ilyophis* was collected and represented a 1.33 ml/l range. *Ilyophis brunneus* was most frequently collected within the 3.89 to 4.28 ml/l oxygen range (900 to 1,100 m) which corresponds to a 0.39 ml/l change in oxygen.

Ilyophis occurs in rather equal numbers throughout its vertical range, therefore, it has a rather wide dissolved oxygen range, comparable to that of *S. oregoni* (1.98 ml/l).

Dissolved oxygen may not influence the movement of *I. brunneus* into deeper parts of the Gulf; however, it may play an important role in affecting the upper limit of vertical distribution of *Ilyophis.* The burrowing habit of *Ilyophis* was reported by Robins (1968), and Richards (1957) found that the oxygen concentration of the water adjacent to the bottom was less than that of the water several meters above the bottom by approximately 0.27 ml/l. The dissolved oxygen of the water next to the bottom at 700 m is probably close to 2.83 ml/l, based on the 3.10 ml/l observed several meters above the bottom. The basic relationship of temperature, metabolic rate, and oxygen requirements could possibly have an important effect on the distribution of *I. brunneus.*

Sediment

Substratum was considered by Thorson (1956) to be the primary factor which influenced the composition of marine level-bottom communities. The animal-sediment relationship was discussed by Sanders (1958); Wigley and McIntyre (1964); Sanders, Hessler, and Hampson (1965); and Day and Pearcy (1968). Of these studies, only Day and Pearcy dealt with benthic fishes, the others were concerned with invertebrate communities. For the invertebrates, a definite correlation between sediment type and distribution was observed. Benthic fishes on the other hand showed a correlation between sediment type and species association; however, some of the species groups did not coincide exactly with a particular substratum.

Table 5 shows the sediment composition with depth for a number of gravity and piston cores taken by TAMU. The continental shelf and slope transition zone (at 200 m) is composed primarily of coarse grained sediments. The slope (200 to 2,900 m) sediments in general are composed of clayey silts, although three stations had high percentages of sand (12.9, 13.2, and 20.2%) and indicate the presence of sediments from the Mississippi Cone.

Synaphobranchus oregoni. The sediment texture of the slope within the 500 to 1,500 m depth interval of *S. oregoni* ranged from 13.2 to 1.3% sand, 16.7 to 14.5% silt, and 82.8 to 78.6% clay. The combined silt-clay fraction ranged from 98.7 to 86.8% (Table 5). The largest numbers of *S. oregoni* were collected from areas where the sand fraction was

3.4 to 1.3% and the combined silt and clay fraction was 98.7 to 96.6%.

Three stations (70A8-8, -11, and -34) within the 500 to 1,500 m depth interval were analyzed for the percent sand, silt, and clay. Stations 70A8-8 and 70A8-11 occurred in an area where numerous captures of *S. oregoni* were reported, and is considered to represent the typical sediment texture over which this species was most frequently found (Table 5). Station 34 occurred in an area where relatively few specimens of *S. oregoni* were taken, despite numerous attempts, and showed some slight differences in textural composition. These textural differences may seem insignificant. However, Sanders (1958) showed that small changes in particle size influenced the composition of invertebrate communities; therefore, the type of food available to *S. oregoni.*

Synaphobranchus affinis. The substratum over which *S. affinis* was collected ranged from coarse-grained (13.2% sand and 86.8% silt-clay) sediment, such as that found on the northeastern slope at the westernmost and northernmost extensions of the distribution of *S. affinis* (Figure 3), to limestone and coral rock which is found along the eastern slope of the Gulf and northern part of the Straits of Florida. The preference by *S. affinis* for a hard substratum was pointed out by Robins (1968), and appears to be confirmed by the distribution established here for this species. It is apparently restricted to the eastern Gulf. Sediment data presented in Table 5 indicate that within the vertical range of *S. affinis* (Figure 2b) in the western section, sediment textures are primarily soft muds composed of 3.4 to 1.3% sand and 96.6 to 98.7% silt-clay. The absence of *S. affinis* from the western Gulf of Mexico could indicate an avoidance of soft sediment by this species.

Synaphobranchus brevidorsalis. The sediment texture within the 1,300 to 1,400 m depth interval of *S. brevidorsalis* was 6.9 to 2.9% sand, 16.7 to 14.5% silt, 80.4 to 78.6% clay, and 97.1 to 93.1% silt-clay combined (Table 5). Gravity core station 71A876 was taken in the vicinity of trawl station 69A1183 (Table 1) where *S. brevidorsalis* was collected and had a 4.3% sand fraction and a 95.7% silt-clay fraction. Core station 70A810 was taken within the 2,100 to 2,200 m depth interval and was near trawl station 1303 where three specimens of *S. brevidorsalis* were collected by the NMFS R/V OREGON. The sediment composition was 3.8% sand, 13.5% silt, 82.7% clay (96.2% silt-clay fraction combined). The data indicated that *S. brevidorsalis* occurred over soft mud bottoms. Sediment of this composition is predominant on the lower part of the western and northern continental slopes of the Gulf (Lynch 1954). The absence of *S. brevidorsalis* from the northern Straits of Florida was considered to be partly due to the hard substratum found in that section of the Gulf. However, since calcareous muds are predominant in the southern part of the Straits of Florida, other limiting factors must be influencing the distribution of *S. brevidorsalis* in this area.

Ilyophis brunneus. *Ilyophis* was collected over the 700 to 1,200 m depth interval which had a sediment composition of 13.2 to 1.3% sand and 98.7 to 86.8% silt-clay (Table 5). Gravity core stations from this depth interval were not analyzed for the silt and clay fractions. Silt and clay are reported as a combined silty sand or clayey silt substrate, which was in agreement with the conditions reported by Robins (1968) for this species in the Straits of Florida. This preference of *I. brunneus* for a soft substratum is reflected in the eel's external morphology which indicates an adaptation for burrowing (Robins 1968).

BIOLOGICAL PARAMETERS

Food Habits

Little information has been published on the food of the Synaphobranchidae. Robins (1968) reported that synaphobranchid eels fed on fish and crustaceans. Information on food habits is reported here to determine if the synaphobranchid eels exhibit any food specialization. The generally accepted ideas on the availability of food in the deep sea are discussed in light of the data obtained from stomach content analyses of 153 specimens of synaphobranchid eels.

Synaphobranchus oregoni. A total of 135 speciments of *S. oregoni* were examined and 53 (39%) were found to contain fish, squid, and crustaceans. Fish and fish parts represented 31% of the identifiable food items; squid and crustaceans each represented 17%. The remaining 35% of the stomach contents could not definitely be classified as belonging to any of the three groups. However, the majority of the food items that were not identifiable were pieces of muscle fiber which resembled fish flesh. Only two of the fish removed were in good enough condition for reliable identification. One was *Canthidermis sufflaman* of the family Balistidae (a surface fish) and the other was a young eel. Based on the condition of *Canthidermis,* it is highly probable that it was captured at the surface and swallowed in the trawl. It appeared from the size, shape, and texture of the fish particles, particularly the vertebrae and jaws removed from the stomach of *S. oregoni,* that no specific family of fish was predominant as a food item.

The squid and crustacean parts tended to be in much better condition for identification than the fish parts. The squid were identified from several mantles and numerous beaks, and all belonged to the order Teuthoides and the suborder Oegopsida. The identifications of two families, Ommastrephidae and Onychoteuthidae are questionable.

The crustaceans removed represented four orders and six families. Decapods were predominant, with sergestid and penaeid shrimp constituting the most numerous food items of the crustaceans. A large flatbacked lobsterette (*Polycheles valida*) was removed from one of the large specimens of *S. oregoni.*

Synaphobranchus brevidorsalis. Of the 10 specimens examined, two (20%) contained food items. Fish eyes were

removed from one eel and a large squid (*Ommastrephes bartrami*) was removed from the other.

Ilyophis brunneus. Eight specimens of *I. brunneus* were examined and two (25%) were found to contain food items. Only one had identifiable contents. It contained one adult isopod (*Aega grarcililes*) which had five young isopods in the brood pouch. *Aega* is a common ectoparasite that is free-living while gravid.

Parasites

Synaphobranchid eels are parasitized by nematodes, trematodes, cestodes, and copepods (Robins 1968). Of the 153 synaphobranchid eels examined for parasites, 131 (86%) were found to be infested. Cestodes occurred most frequently, with nematodes and trematodes appearing moderately. One eel had a parasitic copepod attached to the conjunctive membrane of the eye.

Four new host records for digenetic trematodes and a new species, *Helicometra robinsorum,* were found in the synaphobranchid eels from the Gulf of Mexico (Overstreet and Martin 1974).

Chandler (1954) reports that fish are commonly the intermediate hosts for larval cestodes. It appears probable that the adult cestodes infesting synaphobranchid eels were ingested while feeding on infested fish. This is based on the number of the adult cestodes removed from the abdominal cavity.

The digenetic trematodes are reported to be host specific and usually occur in hosts which are within the same phyla. The intermediate hosts of Digenenea are generally considered to be a mollusk (Manter 1954). Overstreet and Martin (1974) reported *S. oregoni* to be moderately infested with trematodes and stomach content analysis indicated that fish and squid were common food items for *S. oregoni.* It is apparent that both fish and squid are probably important intermediate hosts for the trematodes that infest the synaphobranchid eels.

CONCLUSIONS

The synaphobranchid eels of the Gulf of Mexico are considered an important part of the upper continental slope ichthyofauna, with four species (*Synaphobranchus oregoni, S. affinis, S. kaupi,* and *Ilyophis brunneus*) occurring within the 500 to 1,500 m depth interval and only one species (*S. brevidorsalis*) occurring below 2,000 m.

Synaphobranchus oregoni and *Ilyophis brunneus* were the most frequently captured synaphobranchid eels and occurred rather uniformly throughout the various geographic sections of the Gulf. *Synaphobranchus brevidorsalis* was less frequently collected and occurred only in the northern and western sections. *S. affinis* occurred only in the eastern section. Extensive trawling from the other sections of the Gulf seems to substantiate the distributional pattern shown in Figure 3. The absence of *Histiobranchus* and *Diastobranchus* from the Gulf was reported and is considered valid since 29 trawl stations were taken below 1,800 m, within the reported depth range of both genera.

Vinogradova (1959) considered macro-relief as an important factor affecting the distribution of deep-sea benthic fauna. A thorough investigation of the geomorphology of the continental slopes of the Gulf of Mexico indicates that there are no major topographic features along the slopes with sufficient relief to affect the horizontal distribution of the synaphobranchid eels (Bergantino 1971 and Wilhelm and Ewing 1972).

Synaphobranchid eels of the Gulf of Mexico occurred over a rather narrow range of temperature (7.70 to 4.20°C) compared to that reported by Bruun (1937) for the Synaphobranchidae of the North Atlantic (12.0 to 0.0°C). The largest number of synaphobranchid eels occurred within the 700 to 1,000 m depth interval which had a temperature range of 6.50 to 4.75°C and represented only a 1.75°C change in temperature over 300 m.

A most interesting feature of the temperature regime is the 4.20°C minimum that occurs at approximately 2,000 m. When trying to assess the importance of the effect of temperature on the vertical distribution of the Synaphobranchidae, one has to speculate on the ability of the synaphobranchid eels to cross this few hundredths of a degree temperature gradient to a depth where the temperature begins to increase to a maximum of 4.42°C at approximately 3,700 m.

From the data, one would expect *S. oregoni* to have little difficulty in adapting to a 0.04°C change in temperature. It is therefore suggested that change in pressure is more effective in restricting the downward distribution of *S. oregoni* to the lower slope than temperature. *Synaphobranchus oregoni* would have to adapt to a 667 psi change in pressure to move from 1,500 m to 2,000 m which may be more significant than a 0.04°C change in temperature. *Synaphobranchus affinis,* on the other hand, would have to adjust to a 0.50°C change in temperature and a 1,335 psi change in pressure; therefore, it is felt that the combination of temperature and pressure are limiting factors which restrict *S. affinis* from moving to the lower continental slope. Since *I. brunneus* occupies a position on the slope similar to that of *S. affinis,* temperature and pressure are considered to have comparable limiting effects on both species.

Salinity within the depth range of the Synaphobranchidae decreases from 34.99 ppt at 500 m to 34.88 ppt at approximately 900 m, then increases to 34.95 ppt at 1,500 m. It was slightly more variable horizontally at 500 m than at the deeper depths.

The salinity data from the Gulf tend to support the contention of Bruun (1957) that the small variations in salinity do not appear to have any significant effect on the distribution of Synaphobranchidae either horizontally or vertically. This was determined by comparing the number of synaphobranchid eels collected at approximately the same

depth with the corresponding salinities from nearby hydrographic stations (Table 4).

The dissolved oxygen concentration was shown to increase with depth throughout the depth range of the Synaphobranchidae. The occurrence of the oxygen minimum layer in the eastern and western Gulf was noted and considered to be correlated with the distribution of synaphobranchid eels at the shallower limits of their depth range. This may be due to the basic relationship of increasing temperature with decreasing depth which causes an increase in metabolic rate, resulting in an increased oxygen requirement at depths where oxygen approaches minimum values. The dissolved oxygen concentration was not considered to be a limiting factor on the distribution of synaphobranchid eels into the deeper depths of the Gulf of Mexico.

Although synaphobranchid eels were associated with substrata from clayey silts to hard substratums such as limestone and coral rock, certain species were shown to occur over areas of a particular sediment texture. For instance, *Synaphobranchus oregoni, S. brevidorsalis,* and *Ilyophis brunneus* were collected over sediments which ranged from 13.2 to 1.3% sand, 16.7 to 14.5% silt, and 82.8 to 78.6% clay. *Synaphobranchus affinis* occurred over sediment textures which ranged from coarse-grained sand to limestone.

Synaphobranchid eels have been described as opportunistic feeders or "croppers" (Dayton and Hessler 1972). Based on the size and condition of food items removed from their stomachs, it is assumed that the Synaphobranchidae forage on both live and dead organisms which consist primarily of fish, squid, and crustaceans. It was impossible to identify the fish to family but, based on the size and shape of the numerous fish parts removed, it was evident that several fish families were represented. Seven crustacean families were represented. The squid ingested were confined to the suborder Oegopsida, where two families, Ommastrephidae and Onychoteuthidae, were tentatively identified. If one considers food niche specialization to exist only where a narrow range of food items are ingested, the Synaphobranchidae do not exhibit food niche specialization. However, niche specialization probably occurs with the manner in which the synaphobranchid eels search out and ingest their food.

The availability of food in the deep sea has been reported to be an important limiting resource (Bruun 1957 and Dayton and Hessler 1972). It seems significant that of the 153 synaphobranchid eels examined for stomach contents, 57 (38%) contained food items. Considering the general knowledge that deep-sea fish usually regurgitate stomach content when brought to the surface, this value probably represents a minimum estimate of the percentage of eels which had fed shortly before capture. On an individual station basis, 24 to 33% of the eels examined contained food.

Synaphobranchid eels were heavily infested with cestodes. Nematodes and trematodes occurred moderately. There was one parasitic copepod attached to the conjunctive membrane of the eye of *S. oregoni.*

There were no apparent harmful morphological effects on the synaphobranchid eels infested with parasites. Hopkins (1957) reported that infested hosts usually compensate for loss of nourishment due to parasites by ingesting more food, and that under conditions of food scarcity the infested host might show harmful effects. This tends to indicate that food may not be quite as scarce in the deep sea as has been reported.

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SEEDLING ESTABLISHMENT OF *SPARTINA ALTERNIFLORA* AND *SPARTINA PATENS* ON DREDGED MATERIAL IN TEXAS

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ABSTRACT Effects of fertilizer, elevation, and tidal inundation on seedling establishment of *Spartina alterniflora* and *Spartina patens* were tested at a wave-protected sandy dredged material site, Galveston Bay, Texas. No seedlings that grew from sown seeds became established at elevations below 36 cm (msl) while the greatest number established in the upper tier. Seedlings of *S. alterniflora* were more numerous than *S. patens* in the upper and middle tiers. Naturally occurring seedlings of *S. alterniflora*, which apparently germinated from seeds produced on transplants in adjacent plots, established at all elevations of the site during winter. The average time of tidal inundation at a particular elevation was less during winter than spring. Thus, establishment of plants by seed at low intertidal elevations appears feasible only during low seasonal winter tides and with *S. alterniflora*. Fertilizers did not enhance growth, and high concentrations of fertilizer caused stress to some *S. alterniflora* seedlings.

INTRODUCTION

Means of disposal of dredged material in U. S. coastal environments is a major environmental problem. One beneficial use of dredged material is the establishment of salt marshes. Successful establishment of salt marsh depends on proper location of the dredged material and planting of the material with *Spartina alterniflora* and *Spartina patens* or other intertidal plants (Lewis 1982).

When site conditions are suitable, sowing of seed has been shown to be the most economical method of plant establishment on dredged material (Woodhouse 1979). However, establishment has generally been with transplants since they are more tolerant of waves and currents than seeds and young seedlings (Lewis 1982).

Planting trials were carried out on dredged material to establish a new marsh in Texas (Webb et al. 1978). Seeds of *S. alterniflora* and *S. patens* were used: (1) to test the feasibility of using seeds for marsh establishment; (2) to determine how elevation in relationship to tidal inundation affects seed germination and seedling survival; and (3) to test the effects of various fertilizer treatments on seed germination and seedling growth. The occurrence of seedlings of naturally invading plants also was monitored in permanent quadrats in plots established at the site in 1976 (Webb et al. 1978). Comparisons of the number of naturally occurring seedlings to the number of seedlings that established from sown seeds showed that better establishment occurred during the seasonally lower tides of winter than spring. Fertilizer treatments did not enhance establishment.

DESCRIPTION OF STUDY AREA

A 7.3-ha (18-ac) study site with a northeasterly exposure to Galveston Bay was established in 1976 on dredged material deposited in 1974. Physical and chemical characteristics of the sediment prior to planting were reported by Dodd et al. (1978) and after planting by Lindau and Hossner (1981). Sediments were approximately 98% sand with low amounts of organic material. Because of a fetch length of over 15 miles, a sandbag dike was constructed to minimize wave action on the plantings (Figure 1).

The site was sloped to a 0.7 % grade. The lowest elevation at the site was -4.9 cm (-0.16 ft), in reference to mean sea level (msl), while the upper elevation was +1 m (msl). The mean low water (mlw) for Galveston Bay is actually 0.23 m (0.75ft) above msl while mean high water (mhw) is +0.55 m (1.79 ft) (Lankford and Rehkemper 1969). The mean annual water level is 0.3 m (msl).

MATERIALS AND METHODS

During 1976 at Bolivar Peninsula, Texas, 270 plots (6 × 10 m in size) were established in randomized complete block design with three elevational tiers (Webb et al. 1978). Plots were sprigged in 1976 and others were sown with seed in 1977. Plots received one of five fertilizer treatments. The five fertilizer treatments were mixtures of ammonium sulfate, triple super phosphate, and potassium sulfate. Treatments were: F0–no fertilizer; F1–122 kg N/ha, 122 kg P_2O_5/ha, and 122 kg K_2O/ha; F2–double the amounts of F1; F3–split application of F1; F4–split application of F2.

In preparation for spring seeding, *S. alterniflora* and *S. patens* seeds from local marshes were collected and threshed during fall 1976. *S. patens* seeds were stored dry at ambient room temperature while *S. alterniflora* seeds were stored in an 8% salt solution (S. F. Broome, North Carolina State, pers. comm.) refrigerated at 6°C (Mooring et al. 1971). The percentage of glumes with a caryopsis was determined by physical examination of glumes. Samples of glumes with a caryopsis were placed into petri dishes in the dark at alternating thermoperiods (Mooring et al. 1971) to determine percent viability of filled glumes.

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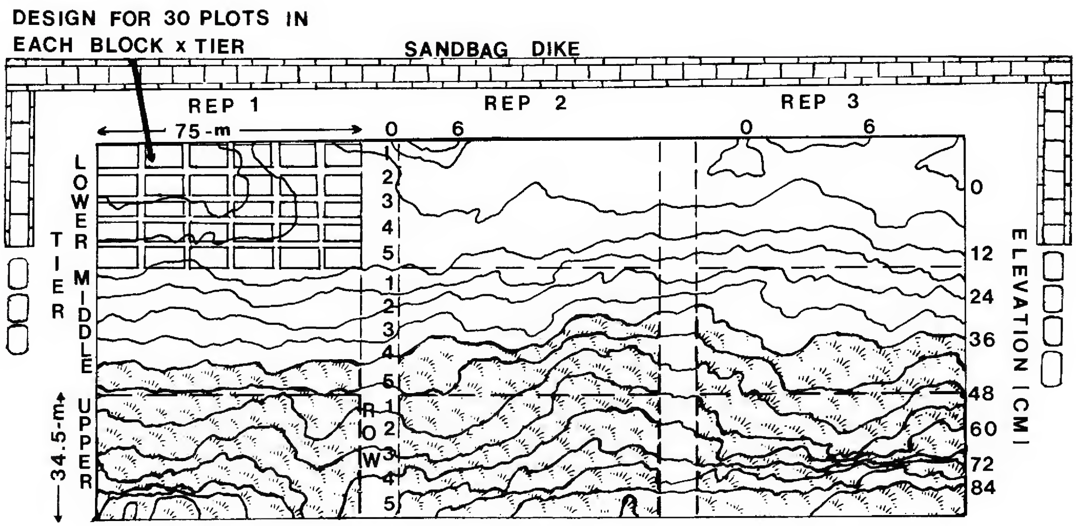

Figure 1. Design of Bolivar Peninsula site showing plot design and 6 cm contour intervals across the site. Establishment of seedlings from hand sown seeds occurred only above 36.6 cm elevation (shaded area).

Ninety unplanted plots, 45 plots sprigged with *S. alterniflora,* and 45 plots sprigged with *S. patens* in 1976 were monitored for plant invasion utilizing three permanent 3-m^2 quadrats in each plot. The data from 24 February 1977 were compared to plots seeded in 1977.

During 21–23 March 1977 at low tides, *S. alterniflora* at 100 viable seeds per m^2, and *S. patens* at 125 viable seeds per m^2 were hand spread in 90 plots along with phosphate and potassium fertilizers. Plots were then disced with a tractor to cover seeds with soil to a depth of 2.5 cm, which is ideal planting depth (Tanner 1979, unpublished data).

Nitrogen as ammonium sulfate was broadcast on the soil surface on 26–28 April 1977 rather than at time of seeding to lessen chances of damage by nitrogen salts. To avoid disturbance of seedlings, nitrogen fertilizer was not disced into the soil. Thus, there was a possibility of loss during tidal exchange and by volatilization. F3 and F4 plots (split rates) were refertilized 26 July by broadcast application.

Nine permanent 0.1-m^2 quadrats were established in each seeded plot (three in each 1/3 of each plot). Seedlings were counted on 14 April, 27 April, 2 June, 27 June, and 14 October 1977 and converted to number per m^2. In addition to measuring density on 27 June and 11–14 October 1977, the following measurements were taken: height of extended leaves; visual estimates of foliage cover; growth characteristics, such as presence of flowers and amount of seed production; and plant stress as exhibited by chlorosis, stunted growth, or wilted leaves. Root and shoot biomass also was randomly sampled in each plot (outside of permanent quadrats) with a 25-cm deep circular coring device with a 0.1-m^2 surface area. Biomass was reported as dry weight after oven drying at 83°C to a constant weight.

Height of tides was automatically punched on ticker tape at 15-minute intervals by a tide gauge established at the site. The raw data was converted by computer programs to histograms showing the percent inundation at 0.1-ft contour intervals for selected time periods, winter and spring. Bench marks, which were established at the site by the Galveston District, Corps of Engineers, allowed the establishment of the tidal datum (1.42 ft below msl) for the tide gauge and furnished the basis for site elevations, which were taken at one corner of each of the 270 plots (Webb et al. 1978).

RESULTS

Natural Seed Germination

The number of seedlings on 24 February 1977 in plots which were monitored for plant invasion indicated that winter germination of *S. alterniflora* seeds had occurred. In the low tier the number of naturally occurring *S. alterniflora* seedlings was much greater in *S. alterniflora* sprigged plots (3.87/m^2) than in *S. patens* sprigged plots (0.28/m^2) or unplanted plots (0.18/m^2). Significant differences ($P<0.0001$) among tiers in the number of naturally occurring seedlings also occurred in *S. alterniflora* sprigged plots (3.87, 2.50, and 0.44/m^2 in lower, middle, and upper tiers, respectively). No significant differences in the number of seedlings were detected between fertilizer treatments.

During the evaluation period scheduled for May 1977, wind elevated tides prevented counts of seedlings in plots at low elevations. However, 0.43 seedlings/m^2, which was the same number as February, were counted in 43 *S. alterniflora* sprigged plots in the upper tier. In the middle tier 0.50 seedlings/m^2 were counted in 19 of the *S. alterniflora* plots as

compared to 2.50 in February. These data indicated that survival and growth of seedlings occurred after germination. Seedlings could not be distinguished from shoots growing from sprigged plants at the June 1977 evaluation.

In early December 1977, many seedlings with two to three leaves and less than 5 cm tall were observed at the Bolivar site. Most seedlings were at the elevation of mean high water (mhw), but many were in soil depressions at lower elevations. Seeds probably were produced at the site since there were at least 92 kg of *S. alterniflora* seeds produced at the site by 14 October 1977 (Webb et al. 1978). Seedlings also were observed in late January 1979 in natural marshes of the area. Additional evidence of winter germination has been presented by Tanner (1979), who reported 14.6 *S. alterniflora* seedlings/m^2 in a marsh several miles from our site. However, Tanner reported that the number of seedlings declined 50% between 27 February and 24 April. Rhizome production caused the number of shoots to increase after 24 April. Seedlings also were located only above 36 cm (msl) elevation and in a wave protected area.

Spring Seed Sowing Experiments

The number of seedlings of *S. alterniflora* was greater than that of *S. patens* in the upper and middle tiers (Table 1). The greatest number of seedlings occurred in the upper tier while no survival for either species was recorded in the lower tier. Examination of contour maps (Figure 1) of the study area showed that no seedlings were observed below an elevation of 36.6 cm (msl). An 84% decline in the number of *S. alterniflora* seedlings in the middle tier occurred between 14 April and 27 April, indicating that most seedlings failed to establish after germination. An increase in the number of *S. patens* seedlings in the upper tier from April to June indicated that germination of *S. patens* occurred several weeks later than *S. alterniflora.*

Fertilizers apparently did not enhance survival or growth since stem density and height of plants were not significantly different among fertilizer treatments. Single (versus split) applications of fertilizers may have been detrimental to seedling growth and reduced chances of survival since plants of F1 and F2 fertilizer treatments of *S. alterniflora* were the only plants to exhibit stress (plant chlorosis and stunted growth). This was significant at $P<0.10$.

TABLE 1

Number of seedling shoots per m^2 in dredged material plots seeded 21–23 March 1977 at 100 viable seeds per m^2.

Species[1]	Tier[2]	Evaluation Date 14 April	27 April	2 June	27 June
Spartina	Lower	0.0	0.0	–[3]	0.0
alterniflora	Middle	5.5	0.9	–	4.2
	Upper	23.8	19.4	21.1	53.4
Spartina	Lower	0.0	0.0	–	0.0
patens	Middle	0.1	0.1	–	1.6
	Upper	1.2	1.5	6.1	33.2

[1] Differences between species significant at $P<0.05$ by analysis of variance F-test on 14 April and 27 April.
[2] Differences between tiers significant at $P<0.05$ by analysis of variance F-test at all evaluations.
[3] Low and middle elevations not evaluated because of high tides.

Plant Measurements on 14 October 1977

The number of shoots of *S. alterniflora* (37.8/m^2) and *S. patens* (30.1/m^2) indicated that seedlings that survived were growing and spreading by rhizomes. However, foliage covered less than 10% of the ground in all treatments. Average shoot biomass was 191 g/m^2 for *S. alterniflora* and 435 g/m^2 for *S. patens.* Root biomass was 325 and 457 g/m^2 for *S. alterniflora* and *S. patens*, respectively.

Immature and mature seed heads on *S. patens* were present 7 September 1977. *S. alterniflora* also produced some seeds by 14 October 1977.

Tidal Differences Between Spring and Winter

During the period 1 January to 20 March 1977 when seedlings became naturally established, mlw was -0.6 cm and mhw was 26.2 cm (msl) (Figure 2). In contrast, during the period from 21 March to 27 April, a 5-week period following sowing of seeds, mhw was 21.3 cm greater in elevation than mhw of the winter time period. Percent time of inundation at each elevation was considerably greater during the latter time period and apparently negatively affected survival of seedlings established from sown seeds.

DISCUSSION

Keeping seeds in place until they germinate is one of the problems when seeds are sown in an intertidal location (Woodhouse et al. 1972). Consequently, April was recommended for sowing of seeds in North Carolina to avoid some of the stormy weather that occurs during March. With waves attenuated by the sandbag dike, sowing of seeds in March appeared ideal due to warmer weather in Texas than North Carolina. However, even with the dike, waves and blockage of light for photosynthesis occurred in association with wind-generated high tides and appeared to be the primary limiting factors for seedling establishment.

Naturally available seeds apparently settled most readily in sprigged plots where some wave protection was provided by plants. The larger number of seedlings in *S. alterniflora* sprigged plots than *S. patens* also indicates that seeds originated from mature plants in *S. alterniflora* plots and not from other marshes.

Saltmarsh inundation does not occur equally throughout the year since a seasonal water level cycle occurs on the northern Gulf coast (Gosselink et al. 1979, Shew et al. 1981). The water regime displays two highs, in spring and in fall, and a winter low (Gosselink et al. 1979, Marmer 1954). Part of the reason for a seasonal fluctuation is that the magnitude of the tidal range is small, being at most

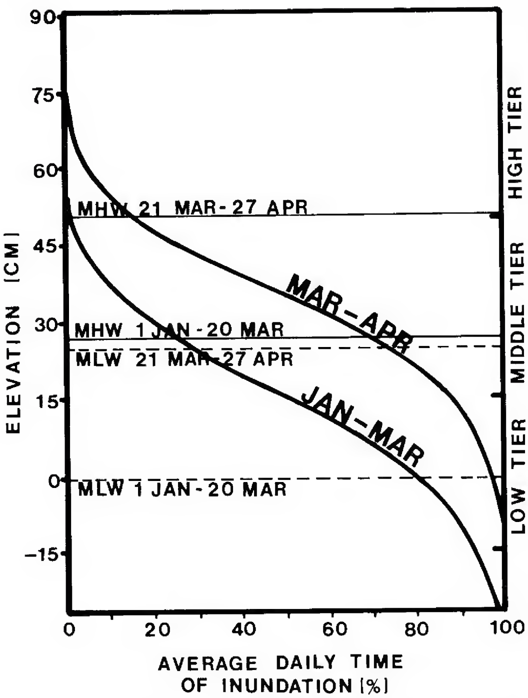

Figure 2. Percent of time each elevation was inundated in marshland plots. Period of monitoring was January 1 to March 20 and March 21 to April 27, 1977. Approximate elevations of each tier are indicated.

places not more than 30 to 40 cm on the average; therefore, the effect of wind on water fluctuation is proportionately large in comparison to other areas where tidal range is greater (Marmer 1954, Shew et al. 1981). Water levels are also affected by seasonal heating and cooling of water and seasonal variability in river discharge (Whitaker 1971, Sturges and Blaha 1976, Gosselink et al. 1979).

Better seedling establishment in winter than spring apparently was because of the seasonally low tides of winter. Galveston Bay waters generally have many suspended soil particles which cause low light penetration into the water; therefore, poor seedling growth may have occurred as photosynthesis of plants was prevented when leaves of seedlings were constantly beneath high tidal waters caused by strong winds during the spring. A coating of clay and silt particles that was observed on many plants also may have hampered photosynthesis and respiration. Because of low tides caused by northerly winds, wave action and light availability were probably not problems to seedlings which germinated in the winter.

Seeds produced during fall 1977 in plots transplanted in 1976 at the Bolivar site were the most likely source of seeds that germinated in early December 1977. The fact that seeds cannot be kept in storage for prolonged periods (Woodhouse and Knutson 1982) rules out delayed germination of seeds planted during the spring. Although Seneca (1974), Woodhouse et al. (1972), and Mooring et al. (1971) state that prolonged cold storage is necessary for germination to occur, Woodhouse and Knutson (1982) reported that cold conditions of 2 or 3 weeks duration will break dormancy. Accordingly, December germination of seeds produced during fall could be expected to occur.

Dry conditions at the highest elevations also may have prevented seedling establishment. Average daily inundation was less than 2.5 hours in all plots in the high tier and some plots were only infrequently flooded. Plants at some of the higher elevations remained in the one or two leaf stage several weeks before dying. Death of plants at the high elevation was not because of hypersalinity of the sediment since soil water salinity was only 11–13 ppt (Webb 1983).

Fertilizers have been shown to enhance growth of transplanted shoots of *S. alterniflora* (Woodhouse et al. 1972, Garbisch et al. 1975), but fertilizers apparently were not beneficial to plants in this study. Despite a delayed application, nitrogen fertilizers did not enhance growth of plants and may have caused some stress. The probable cause of injury was soluble salts from nitrogen, phosphorus, and potassium fertilizers, which may cause injury when applied too close to seedlings (Tisdale and Nelson 1966). The possibility of fertilizer salt damage is further substantiated by Garbisch et al. (1975), who reported detrimental effects and increased mortality when fertilizers were applied to *S. alterniflora* seedlings at the time of transplanting.

The value of using seeds is demonstrated by the greater number of shoots in plots with good survival when compared to the number of shoots in sprigged plots after equivalent evaluation periods (Webb et al. 1978). However, the inability to establish seeds at all elevations without a great chance of failure makes the use of sprigs more reliable than seeds. Establishment from seeds may be possible at all elevations under a low tidal regime, which may occur only during the winter on the U. S. Gulf of Mexico coast.

CONCLUSIONS

Successful establishment of seedlings of *S. alterniflora* and *S. patens* on dredged material is prevented by factors associated with tidal inundation. This was demonstrated by lack of seedling survival at low intertidal elevations during March while establishment of seedlings occurred at all elevations of the study site during low tidal regimes of winter. Therefore, if sowing of seeds is to be accomplished, winter is the best season because of favorable low tides.

Fertilizers did not increase survival or growth. In fact, heavy applications of fertilizer resulted in slight salt damage to *S. alterniflora.*

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Amphipods of the Family Ampeliscidae (Gammaridea). III. *Ampelisca parapacifica,* a New Species of Amphipod from the Western North Atlantic with the Designation of a Substitute Name for *A. eschrichtii pacifica* Gurjanova, 1955

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AMPHIPODS OF THE FAMILY AMPELISCIDAE (GAMMARIDEA) III. *AMPELISCA PARAPACIFICA,* A NEW SPECIES OF AMPHIPOD FROM THE WESTERN NORTH ATLANTIC WITH THE DESIGNATION OF A SUBSTITUTE NAME FOR *A. ESCHRICHTII PACIFICA* GURJANOVA, 1955

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ABSTRACT A new species of benthic amphipod, *Ampelisca parapacifica,* is described from the southeastern Gulf of Mexico and compared with the closely allied *Ampelisca pacifica* Holmes, 1908, from the eastern Pacific. The distinctive form of the third uropod separates this species pair from other members of the "macrocephala" subgroup of the genus *Ampelisca* Kroyer, 1842. *Ampelisca parapacifica* is distinguished from *A. pacifica* by antenna I peduncle segment 2 less than twice the length of article 1 and uropod 1 peduncle shorter than the rami. Previous Atlantic records of *A. pacifica* are assigned to the proposed new species. The Pacific populations of *A. eschrichtii pacifica* Gurjanova, 1955, were elevated to the species rank by Karaman, unaware that the name *A. pacifica* was preoccupied. A substitute name, *A. karamani,* nomen novum, is designated for the form described by Gurjanova.

Twelve of the 17 species of the genus *Ampelisca* Kroyer, 1842, reported from the Gulf of Mexico were originally described from the Pacific Ocean (Barnard 1954b, Goeke and Heard 1983). Recently, one of these 12 nominal species has been elevated to species rank in the western Atlantic (*Ampelisca bicarinata* Goeke and Heard, 1983). *Ampelisca pacifica* Holmes, 1908, has been reported with a transpanamic distribution by several authors (Barnard 1954b, Mills 1965, McKinney 1977). However, a more detailed comparison of specimens from waters off California and the southeastern Atlantic coast indicate that the western Atlantic populations previously assigned to *A. pacifica* represent a new species.

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Ampelisca parapacifica new species
(Figures 1, 2 and 3)

Ampelisca pacifica: Barnard, 1954b, p. 5; Mills, 1967, p. 649 (not *A. pacifica*: Karaman 1975).

Material Examined

Holotype – 1 ♀, 8 mm, USNM 195114, 27°52′31″N, 83°33′56″W, 17 June 1974, 33 m, clayey, sandy silt.

Paratypes – USNM 195116: 1 ♂, 4 ♀♀, same collection data as holotype; USNM 195124 2 ♀♀ (1 ovig), 24°47′30″N,

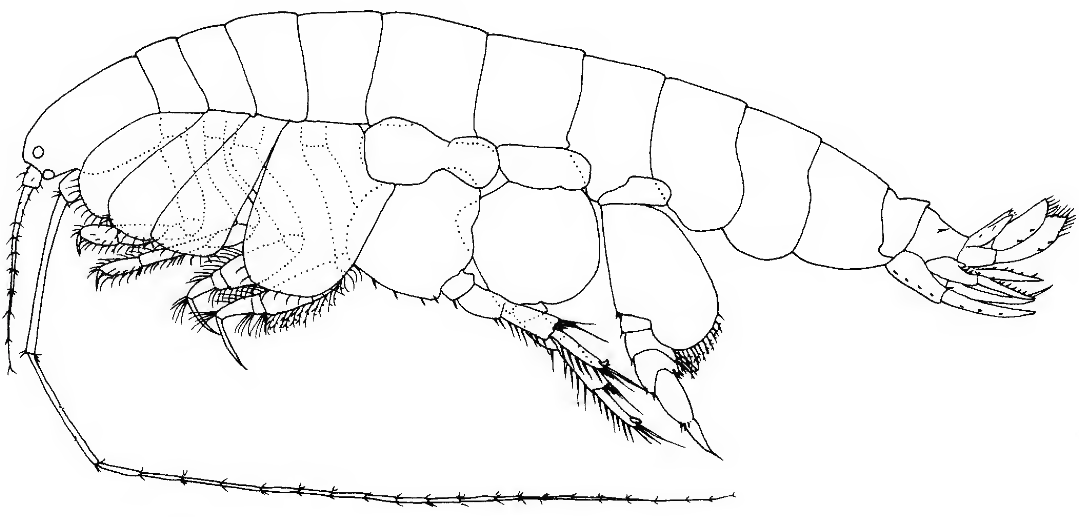

Figure 1. *Ampelisca parapacifica,* new species.

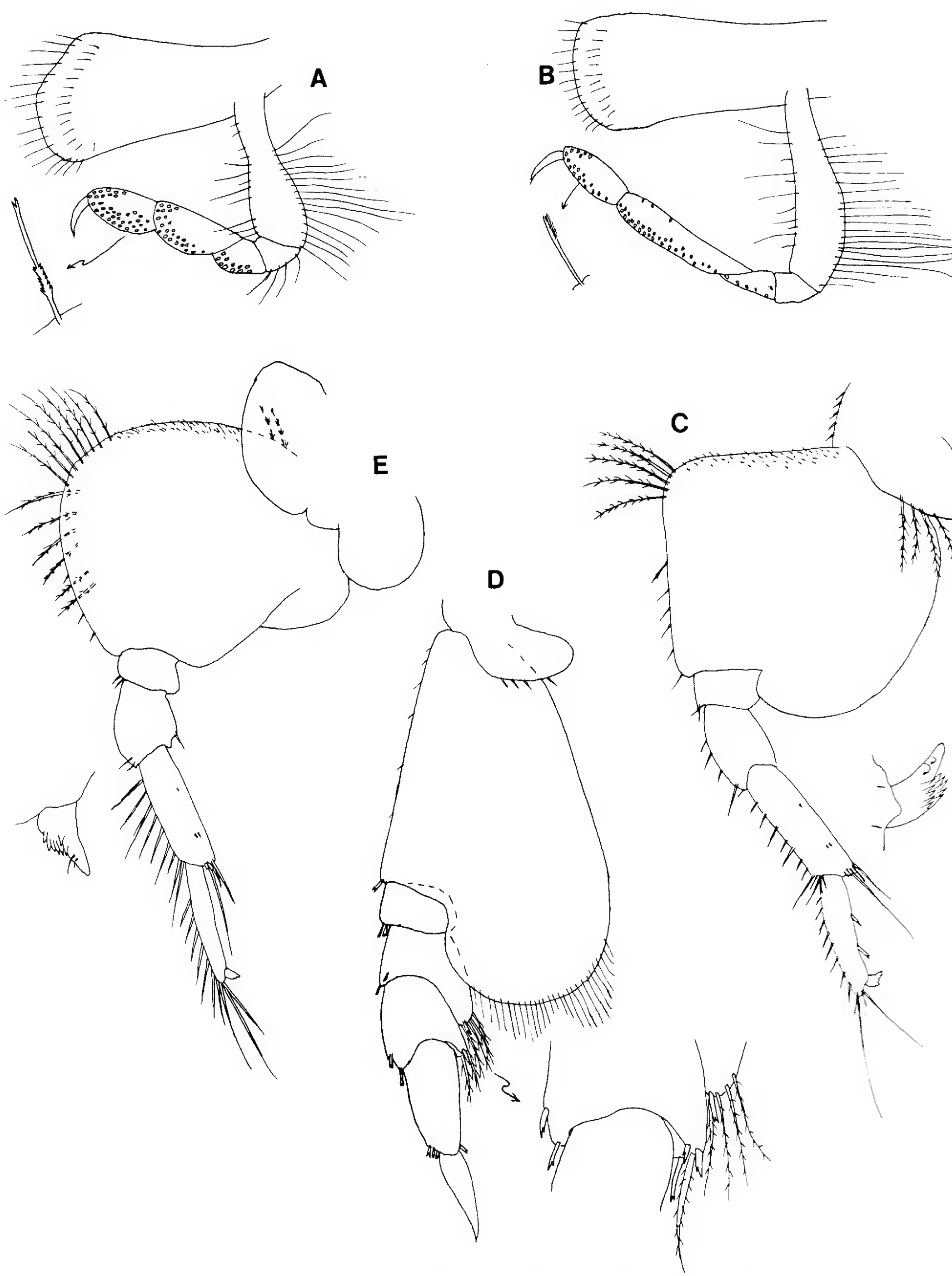

Figure 2. A. Pereopod 1; B. Pereopod 2; C. Pereopod 6; D. Pereopod 7; E. Pereopod 5.

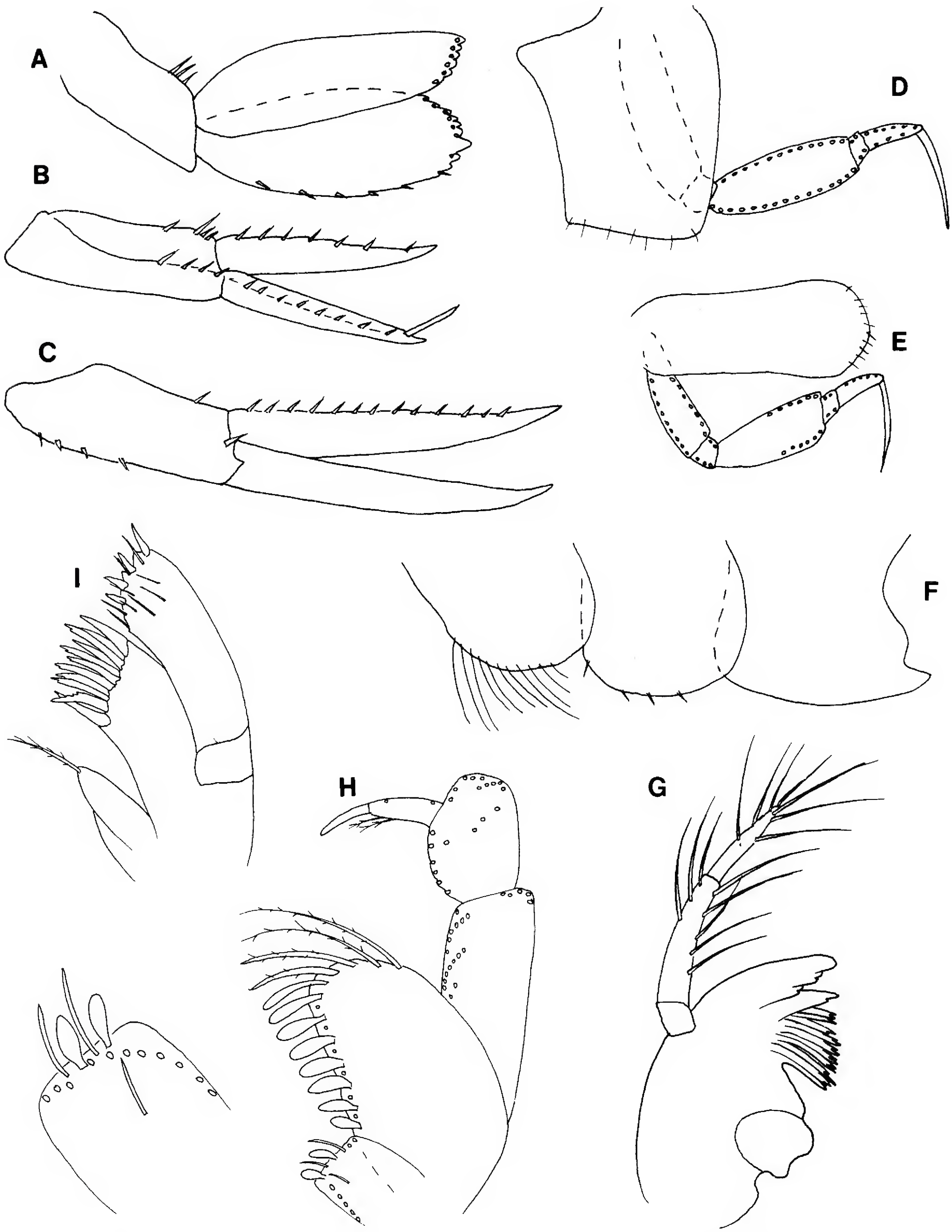

Figure 3. A. Uropod 3 (setae omitted); B. Uropod 2; C. Uropod 1; D. Pereopod 4 (setae omitted); E. Pereopod 3 (setae omitted); F. Epimeral Plates 1–3; G. Mandible; H. Maxilliped; I. Maxilla 1.

83°13′15″W, 8 April 1981, 59 m, medium sand (illustrated); USNM 195119 1 ♂, 27°50′00″N, 82°25′00″W, 17 June 1974, 32 m (illustrated); USNM 195115 1 ♀, 26°16′30″N, 82°38′00″W, 28 July 1981, 26 m, very fine sand; USNM 195118 2 ♀♀, 25°47′15″N, 82°25′00″W, 12 February 1982, 26 m, very fine sand; USNM 195123 1 ♀, 25°47′15″N, 82°25′00″W, 8 November 1980, 26 m, very fine sand; USNM 195122 2 ♀♀, 25°45′30″N, 83°11′00″W, 28 April 1981, 54 m, medium sand; USNM 195117 1 ♀, 25°45′30″N, 83°11′00″W, 27 July 1981, 54 m, medium sand; USNM 195120 1 ♀ (1 ovig), 25°47′00″N, 83°58′00″W, 27 July 1981, 135 m; USNM 195121 2 ♂♂, 27°56′00″N, 83°27′29″W, 17 June 1974, 32 m; AHF 8010 (Allan Hancock Foundation), 8♀♀, 25°46′00″N, 82°24′00″W, November 1980, 26 m, very fine sand; MNHN Am 2442 (Muséum National d'Histoire Naturelle, Paris), 8 ♀♀, 25°46′10″N, 82°24′00″W, November 1980, 26 m, very fine sand; GCRL 1122 (Gulf Coast Research Laboratory, Ocean Springs, Mississippi), 4 ♀♀, 28°41′59″N, 84°26′30″W, 9 June 1974, 38 m.

Other material – 1 ♀, 29°53′30″N, 88°12′28″W, 1975, 32 m, sandy silt; 3 ♀♀, 29°48′05″N, 88°13′08″W, 18 May 1974, 35 m; 1 ♂, 2 ♀♀, 28°00′38″N, 83°44′49″W, 16 May 1974, 38 m; 1 ♂, 12 ♀♀, 27°57′30″N, 83°42′29″W, 16 June 1974, 38 m; 1 ♂, 6 ♀♀, 27°57′00″N, 84°49′59″W, February 1978, 189 m, silty very fine sand; 1 ♀, 27°57′00″N, 84°48′00″W, August 1977, 189 m, silty very fine sand; 1 ♀, 27°57′31″N, 83°33′59″W, November 1977, 34 m, clayey sandy silt; 3 ♀♀, 27°45′30″N, 83°25′30″W, 13 June 1974, 42 m; 5 ♀♀, 26°25′00″N, 82°58′00″W, Cruise 22, 33 m, fine sand; 4 ♀♀, 26°24′57″N, 82°38′00″W, 6 November 1980, 26 m, very fine sand; 1 ♀, 26°16′45″N, 83°47′45″W, 4 November 1980, 90 m, fine sand; 2 ♀♀, 26°16′45″N, 83°47′45″W, 30 April 1981, 90 m, silty very fine sand; 4 ♀♀ (1 ovig), 26°16′15″N, 83°00′13″W, 5 November 1980, 48 m, fine sand; 1 ♀, 25°47′15″N, 82°25′00″W, 28 July 1981, 26 m, very fine sand; 1 ♀, 25°40′00″N, 84°15′00″W, November 1977, 180 m, silty very fine sand.

Diagnosis – Lower margin of head deeply concave, 2 pair of corneal lenses, antenna I reaching just past articulation of antenna II peduncular segments 4 and 5, length ratio of antenna I peduncular segments 100:150:80, antenna II is 2/3 length of body, ratio of length of peduncular segments 4 and 5 of antenna II is 100:90; inner plate of maxilliped with 2 chisel teeth and 2 setal spines, maxilla 2 with about 10 facial spines; mandible with 10 accessory blades, terminal article of palp 2/3 length of second article; coxal plates 1 and 2 with posterodistal slit; posterior margin of merus of pereopod 3 with setae in distal 1/2 only; dactyli of pereopods 5 and 6 with numerous accessory teeth, epimeral plates 1 and 2 rounded, plate 3 with strong posteroventral tooth and small superior lobe, urosomite 1 dorsally sinuous; outer ramus of uropod 1 devoid of spines, outer ramus of uropod 2 with long terminal spine, outer ramus of uropod 3 oval; uropods 1 and 2 equal in length; gills of female sac-like.

Description

Female (8 mm) – Head equal to first 2 1/2 body segments in length; 2 pair of corneal lenses, 1 at lower front margin and 1 posterodorsal to insertion of antenna I, eyes heavily pigmented; lower margin of head deeply concave for 1/4 length then oblique. Antenna I peduncular segment 1 little inflated with few scattered setae, second and third segments linear, ratio of length of peduncular segments 1 to 3 is 100:150:80; flagellum of 7 segments, extending 1/3 length of fifth peduncular segment of antenna II. Antenna II peduncular segments 1–3 compact, segments 4 and 5 elongate with scattered setae, ratio of lengths of segments 4 and 5 is 100:90, flagellum of 21 articles, extending 2/3 length of body.

Upper lip, lower lip and maxilla 1, all normal for genus or without diagnostic features. Maxilla 2 inner plate with single apical seta, outer plate with 11 terminal spines, all with accessory teeth, palp segment 2 with about 10 facial setal spines and 4 blunt apical spines. Left mandible with well sclerotized molar process, 10 accessory blades, lacinia mobilis with 5 teeth, incisor with 7 teeth, palp segment 1 short, segment 2 elongate with lateral margins lined with scattered setae, segment 3 is 0.6 times length of second article with 5 medial simple setae and 3 terminal simple setae. Maxilliped inner plate short, rectangular distally with submarginal row of plumose setae and facial setal spine, distal margin with 2 chisel teeth and 2 setal spines, outer plate with 9 chisel teeth medially, 3 terminal plumose spines, most chisel teeth with accessory setal spines, outer plate reaching to the end of palp article 2, outer plate lateral margins lined with cilia, palp normal for the genus, with simple setae lining margins, third palp article clavate.

Coxal plates 1 and 2 with marginal and submarginal rows of plumose setae, coxal plates 3 and 4 with scattered marginal setae; coxal plates 1 and 2 with slit at posteroventral angle.

Pereopod 1 basis inflated distally, posterior margin with long simple setae, ischium subtriangular with several posterodistal plumose setae, merus diamond-shaped with long plumose setae ventrally and anterodistally, carpus inflated, with plumose and comb setae or ventral and anterior margins; propodus inflated, width 0.7 times length, with barbed spinules and bifid setae on palm and long simple setae dorsally; dactyl short, length 0.55 length of propodus with 3 accessory spinules on ventral margin.

Pereopod 2 basis inflated distally, anterior and posterior margins with elongate setae, ischium subquadrate with few setae, merus elongate, underriding carpus slightly, few plumose setae on ventral margin, carpus elongate, width 0.2 times length, ventral margin with elongate plumose setae propodus elongate; propodus elongate, width 3 times length, ventral margin with barbed spinules and elongate simple setae, dorsal margin with few plumose setae; dactyl width 0.5 times length of propodus, with 4 accessory comb spines.

Pereopod 3 slightly smaller than 4, but similar in shape, different in setation; basis elongate, little inflated, pereopod 3 with few scattered short setae on anterior and posterior margin, pereopod 4 with long plumose setae on posterior margin; ischium subquadrate, setose on pereopod 4; merus elongate, inflated, pereopod 3 with distal plumose setae on both margins.

Pereopod 4 with anterior and posterior margins lined with long plumose setae; carpus subquadrate, propodus subrectangular, margins with plumose setae; dactyli elongate, lanceolate, longer than propodus and carpus combined.

Pereopod 5, coxa with well developed anterior and posterior lobes devoid of setae, anterior lobe of basis with 4 long plumose setae at anterior angle and with small simple setae scattered along margin, posterior margin faintly bilobate, dorsal lobe well developed with straight posterodorsal margin, ventral lobe poorly developed, both devoid of setae, ischium short with 2 small setae anterodistally; merus approximately 2 times length of ischium with simple long spine anterodistally; carpus subrectangular, anterior margin lined with 6 long simple setae and single long distal spine, posterodistal margin with set of 5 spines increasing in length, longest subequal to propodus, a set of small spines submarginally at midlength; propodus subrectangular, anterior margin with 5 long comb setae, posterior margin with single short spine, 3 spines terminally, 2 simple and 1 comb; dactyl stubby, subterminal with 7 accessory teeth and main fang.

Pereopod 6, coxa lobate posteriorly with 3 plumose setae, anterior margin straight with 3 long plumose and 4 short simple setae; basis, anterior margin bent at nearly 90° angle, 4 long plumose setae at angle, scattered simple setae along entire margin, single spine distally, posterior lobe very well developed, devoid of setae, ischium short with single simple seta anteriorly, merus approximately 2 times length of ischium with a simple seta and spine at anterodistal margin, carpus subrectangular with 4 spines on anterior margin, cluster of 4 spines anterodistally, posteriorly with single and pair of submarginal spines, posterodistal angle with cluster of 6 comb spines increasing from short to a length subequal to propodus, propodus subrectangular with single submarginal posterior spine and 6 anterior spines, cluster of 4 spines terminally with the longest greater than length of propodus, dactyl with numerous accessory teeth to main fang.

Pereopod 7, coxa with anterior margin straight, posterior margin lobate with scattered short simple setae, anterior margin of basis straight with single spine distally, posterior margin broadly rounded distally, extending to end of merus, plumose setae only on distal margin, ischium subrectangular with 2 short spines anterodistally, merus bilobate, anterior lobe with single spine distally, posterior lobe with 4 long plumose setae and a single spine distally, carpus with anterior lobe better developed than posterior lobe, anterior margin with spine at 3/4 length and distally, posterior margin with 4 short distal spines and plumose seta, propodus length less than twice greatest width, 4 anterodistal and 3 posterodistal short spines, dactyl attenuated, curved forward.

Dorsum of pereosome and pleosome smooth. Epimeral plate 1 with sinuous anterior margin, rounded posteriorly, several long plumose setae in anterior and ventral margins. Epimeral plate 2 with rounded anterior and posterior margins, few scattered spinules on ventral margin. Epimeral plate 3 rounded anteriorly, slightly concave on anterior margin, ventral margin slightly convex, very strong tooth posteroventrally with small superior lobe, posterior margin sinuous. Urosomite 1 with sinuous dorsal carina, urosomites 2 and 3 low, fused.

Uropod 1 equal to 2, peduncle 4/5 length of rami, 4 short lateral facial spines ventrally, single spine dorsally at articulation with outer ramus, dorsolateral margin sinuous, devoid of spines; outer ramus without dorsal spines but with 3 short submarginal facial spines along ventral margin, inner ramus with numerous spines. Uropod 2 peduncle nearly as long as rami, outer margin with 4 spines in distal 1/2, inner margin with 4 spines, outer ramus with 8 spines along margin and a long subterminal spine 1/3 length of ramus, inner ramus with 2 submarginal ventral spines, plumose and simple setae on distal margin, dorsal margin devoid of setae. Uropod 3 peduncle short with 2 dorsal spines, outer ramus broad proximally, tapering slightly to blunt apex with plumose setae and ventral spinules; inner ramus oval with ventral spinules, plumose setae on distal margins. Telson deeply cleft, 1/2 of length, 2 pair of short dorsal spines, apices with 1 bifid spine and a companion seta on each lobe.

Male – Differs from female most notably by: (1) antennae with increased setation, (2) antenna I nearly as long as peduncle of antenna II, (3) antenna II as long as body, (4) pleosome more massive, (5) inner rami and peduncles of uropods 1 and 2 much more spinose, (6) dorsal boss and carina of urosomite 1 more massive, (7) distal spine of outer ramus of uropod 2 smaller, and (8) gills strongly pleated.

Variation – Infraspecific variation observed in the specimens of *A. parapacifica* we examined was slight, mostly attributable to sexual dimorphism and stage of development. Variation was noted in the length of the antennae, development of the carina of urosomite 1 and the dorsalmost process on the posterior margin of epimeral plate 3. Juvenile and subadult individuals often possess antenna II as long as the body or longer. This condition is normal within this family. Minor variation in the shape of the carina of urosomite 1 was noted in mature individuals and is also normal. In some specimens, the superior lobe on the posterior margin of epimeral plate 3 was even smaller than normal. In these individuals, the posterior margin of epimeral plate 3 is only slightly sinuous with no "lobe" evident. No relationship was observed with age or sex and degree of variation in the latter two characters.

Etymology – The specific name is derived from the Latin "para-," close and the specific name "pacifica". The name is in reference to the close affinity of the species with *A. pacifica* Holmes, 1908.

Remarks – *Ampelisca pacifica* Holmes, 1908, has been

TABLE 1

Comparison of selected morphological characters.

	Ampelisca parapacifica	*Ampelisca pacifica*
Ratio of length of Antenna I peduncular segments	100:150:80	100:225:125
Ratio of length of Antenna II peduncular segments 4 and 5	100:90	100:66
Maxilla 1 palp segment 2	4 large terminal spines	5 large terminal spines
Mandibular palp segment 3	5 lateral setae	3 lateral setae
Pereopods 3 and 4	equal	pereopod 4 more massive
Dactyli of pereopods 3 and 4	longer than combined length of propodus and carpus	equal to combined length of propodus and carpus
epimeral plate 3	superior lobe evident	superior lobe very reduced
Lateral margin of urosomite 3	oblique	acuminate
Uropod 1 length	peduncle shorter than rami	peduncle longer than rami
Telson spines	1 pair	2 pairs

reported from the waters of Southern California by Holmes (1908) and Barnard (1954a, 1966) in 24 to 496 m depth. A subsequent record from Caledonia Bay, Panama, by Barnard (1954b) is the first reference for this species from the western Atlantic. Since that report, *A. pacifica* has been listed from the western Atlantic by Mills (1965, 1967) and McKinney (1977).

Ampelisca parapacifica is a member of the "macrocephala" subgroup and is closely related to numerous species which share the head shape, form of pereopod 7, posterior process of epimeral plate 3 and general shape of the mouthparts. However, the unique combination of characters given in the diagnosis easily distinguishes it from other members of the subgroup. *Ampelisca parapacifica* differs from *A. macrocephala* Liljeborg, 1852, *A. unsocalae* Barnard, 1960, and *A. careyi* Dickinson, 1982, by the deeply concave lower margin of head, shorter antenna I and ovoid uropod 3. It may be distinguished from *A. cristata* Holmes, 1908, *A. cristoides* Barnard, 1954, and *A. bicarinata* Goeke and Heard, 1983, by the very strong tooth on the posterodistal margin of epimeral plate 3, ovoid uropod 3 and the lack of dorsal carinae of pleosomite 3 and urosomite 1. *Ampelisca parapacifica* is distinguished from *A. brevisimulata* Barnard, 1954, and *A. verrilli* Mills, 1967, by the subequal uropods 1 and 2, small superior lobe of epimeral plate 3, notched anterior margin of segment 5 on pereopod 7 and foliaceous uropod 3. *Ampelisca parapacifica* is separated from *A. panamensis* Barnard, 1954, and *A. parapanamensis* Barnard, 1954, by the strong process of epimeral plate 3, foliaceous uropod 3, and the shorter antenna I.

Ampelisca parapacifica is most closely related to *Ampelisca pacifica* Holmes, 1908, with which it shares a broad, oval uropod 3. Only 6 described species possess this character. *Ampelisca rostrata* Spandl, 1924, *A. misakiensis* Nagata, 1959, *A. byblisoides* Barnard, 1925, *A. statenensis* Barnard, 1932, and *A. hessleri* Dickinson, 1982, all share this uropodal feature but are easily distinguished by different leg shapes. *Ampelisca dentifera* (sensu Schellenberg 1931) possesses the oval uropod 3 and leg shape of *A. parapacifica* but can be separated by the more massive pleon segment 4, antenna I equal in length to peduncle of antenna II and shorter article 1 of antenna I. Table 1 presents selected characters which distinguish *A. parapacifica* from *A. pacifica.*

The geographic range of *A. parapacifica* includes Cape Lookout, North Carolina (Mills 1967), the eastern Gulf of Mexico and southward to Caledonia Bay, Panama (Barnard 1954b). *Ampelisca parapacifica* appears to be widespread in the warm temperate and tropical waters of the northwestern Atlantic.

Ecological notes – *Ampelisca parapacifica* occurs in abundance on the sandy carbonate bottoms of the southeastern Gulf of Mexico. Collection data indicate the species is most often collected on substrata ranging from medium sand to silty, very fine sand composed primarily of carbonates. Bathymetric range of this material is 24 to 189 m. It is probable the species will be found below this depth as the 189 m record represents the deepest station sampled.

Taxonomic status of *Ampelisca eschrichtii pacifica* Gurjanova, 1955.

Karaman (1975) described *Ampelisca richardsoni* from Anvers Island in the Antarctic as very closely related to *A. eschrichtii* Kroyer, 1842. In that work he shows no *Ampelisca* species has a true bipolar distribution but that sibling species occur in both polar regions. *Ampelisca richardsoni* was differentiated from *A. eschrichtii* and *A. eschrichtii pacifica* Gurjanova 1955. This latter taxon exhibited sufficient characters that Karaman elevated it to the full species rank, apparently unaware that the name "pacifica" was occupied. *Ampelisca pacifica* Holmes, 1908, has clear precedence and we designate the name *Ampelisca karamani,* nomen novum, for *Ampelisca pacifica* Gurjanova, 1955. This species is named for Dr. Gordon Karaman in recognition for his significant contributions to the taxonomy and systematics of the Amphipoda.

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Autecology of the Black Needlerush *Juncus roemerianus*

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AUTECOLOGY OF THE BLACK NEEDLERUSH *JUNCUS ROEMERIANUS*

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ABSTRACT *Juncus roemerianus* generally occupies the upper half of the intertidal plane and covers about 92% or 25,000 hectares of marsh in Mississippi. The vegetative canopy is best described as a series of disjunct and intergrading populations. Considerable phenotypic variation and differences in standing crop exist between populations. *J. roemerianus* has very wide environmental tolerances in comparison to all other tidal marsh angiosperms. Soil types inhabited by the rush range from very sandy to highly organic muds and peats, which may vary in the concentration of nutrient elements (nitrogen, phosphorus and potassium). Neither soil type, nutrient concentration, water content, pH nor elevation can be used to distinguish the habitat of *J. roemerianus,* because similar conditions are found in areas occupied by pure or almost pure monotypic stands of other plant species. Soil water salinity is cyclic in all populations of *J. roemerianus* examined and salinity appears to be the major edaphic factor affecting growth and distribution of the rush. The greatest concentration and fluctuation of salt content occurs in the near-surface soil layer and the lowest concentration of salt and most stable soil water regime occurs at increasingly lower depths. Experimental evidence indicates that the rush grows best in fresh water, without competition, and cannot tolerate continuous salinities greater than 30 ppt. Soil organisms which detrimentally affect the rhizomes are major factors limiting distribution of the rush into freshwater areas. Salt concentrations in the soil solution of 35–360 ppt occurs frequently in some near-surface marsh soil layers. *J. roemerianus* growing on "salt flats" apparently survives near-surface hypersaline soil water (90–360 ppt) because of deeply penetrating, specialized roots. About five billion seeds of *J. roemerianus* are produced annually in Mississippi tidal marshes, but few rush seedlings are found. Germination requires light, and seedling establishment is the vulnerable stage in the life cycle of the species. Vigorous mature stands are maintained by rhizome growth and the frequent removal of dead-standing leaves by physical factors such as storms, heavy rains, tides, and currents.

INTRODUCTION

Juncus roemerianus Scheele dominates about 25,000 hectares or 92% of tidal marsh in Mississippi (Eleuterius 1972) and about 320,000 hectares or 25% of tidal marsh throughout North America (Eleuterius 1976a). Daubenmire (1947) stated that autecological studies were important because the factors affecting the most important plants of a community, including various stages in their life cycle, must be understood before the ecology of the community can be understood. Autecological studies upon angiosperms inhabitating aquatic habitats are seriously lacking, but essential in understanding the peculiar adaptation of various species (Davis and Heywood 1963, Alexander 1971). Baker (1959) stated that discovering crucial environmental factors that affect the plant may provide valuable information concerning the evolution of the taxa. Furthermore, basic autecological information provides a foundation from which taxonomic studies, genetic studies, population biology, studies on the breeding system, and other more specific studies on ecological relationships can be initiated. An adequate understanding of adaptation and the factors regulating important species over large tracts of salt marsh would also provide the most valuable information to expediently assess and manage these complex and valuable ecosystems in view of continuous loss, pollution, and the increased pressure of human population growth on coastal areas.

The objectives of the present study are (1) to examine the general characteristics of the intertidal habitats occupied by *Juncus roemerianus* and (2) to evaluate how they are related to the rush and to areas inhabitated by other marsh plants. From this general examination, (3) identify and (4) provide experimental data on those exceptional factors affecting the growth and distribution of *J. roemerianus.*

This approach rapidly eliminates those minor factors, either limiting or favorable, which can not be strongly related to the distribution of the rush or account for variations in growth between populations.

MATERIALS AND METHODS

Twenty-six populations of *Juncus roemerianus* were sampled in the tidal marshes along the coast of Mississippi (Figure 1). Standing crop was determined by counting and clipping shoots from four or more rectangular (0.5 × 2.0 m) frames and square ($0.25m^2$) frames in seven populations. Clipped samples were subsequently separated into living and dead components and the number of leaves counted. Seventy-five of the longest living leaves in each population were selected randomly and measured for stand height (average maximum leaf length attained). Standing crop of erect shoots was obtained by drying to constant weight in a forced air oven at 50°C for 24 hours and then weighing.

Soil water salinity was determined from soil cores about 50 cm in length, obtained by using thin-walled stainless steel tubes with an inside diameter of 72 mm. Three cores were taken seasonally from each habitat. Slices of the core about 2 cm thick were taken from the top or surface layer and at positions equivalent to 30 and 45 cm depths. Soil water was extracted from these slices by vacuum filtration.

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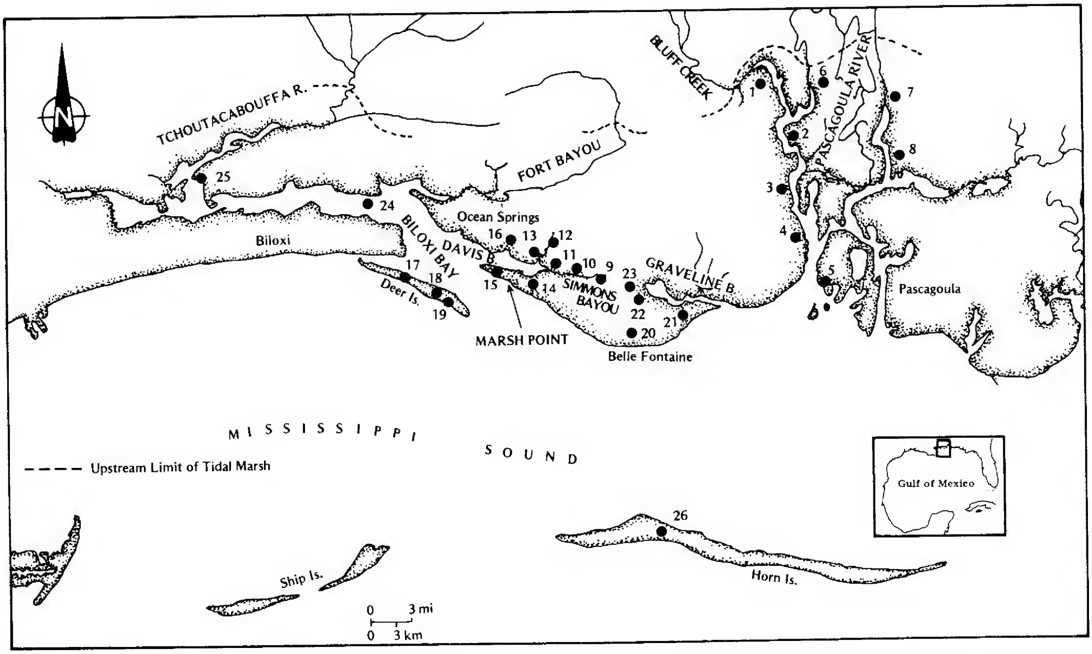


Figure 1. Map of the study area on the Mississippi coast. The location of populations of *Juncus roemerianus* studied are indicated by numbers.

All samples were subjected to uniform vacuum extraction (60 cm of mercury). Soil water salinity was determined with an American Optical refractometer, Model 10402 with a direct-read-out scale in ppt, and compared to determinations made with a Martex salinometer and a conductivity bridge. Soil water was also extracted by the method described by Eleuterius (1980a) and compared to the vacuum filtration method. No significant differences were found between the three methods used to determine salinity. Hydrogen ion concentration (pH) was determined in the field with a Corning model 6 portable meter and compared to wet soil samples determined with an Orion meter in the laboratory. A total of 234 soil samples were taken. The same soil cores were used for determinations of salinity, organic matter content, nitrogen, phosphorus, and potassium from the 26 populations of *Juncus roemerianus*, using standard methods described by Black (1965). Similar soil samples were also gathered and analyzed from populations of *Spartina alterniflora, Distichlis spicata, Scirpus olneyi,* and *Cladium jamaicense.*

Elevations in the marsh were determined using a surveyor's transit and stadia rod in reference to a bench mark located in the sea wall on East Beach, Ocean Springs, Mississippi, described in detail in Eleuterius and Eleuterius (1979).

To determine if light was required for germination, seeds of *Juncus roemerianus* were collected, placed on solidified agar in petri dishes in light and dark boxes at room temperature and placed under Gro-lux fluorescent lamps at 3875 lux (360 foot candles). Seeds from perfect and pistillate flowers were collected from a population in the Davis Bay area. Approximately 1200 seeds were tested.

To test the general viability of seed, about 8400 seeds representing hermaphroditic and female components of seven populations were sown on solidified agar in petri plates and placed under Gro-lux lamps. Seeds were also floated on saline solutions and placed under continuous light for 6 weeks to test the effect of salinity on germination. Counts of germinated seed were made weekly.

Artificial sea mix (Rila) was used to prepare saline solutions of different concentrations to test the effect of salinity on germination of seed from both plant types and to determine the effect of salinity on vegetative growth of mature plants. Plants were selected randomly in each of several different populations and grown in a mixture of 1/2 sand and 1/2 commercial organic potting soil. Then the porous clay pots containing the plants and soil mixture were placed in large plastic buckets containing salt solutions of different concentrations. Water levels were adjusted 3 cm below the soil surface in each pot. Four replications of each treatment were used. Controls were grown in untreated tap water. Water lost through evaporation and transpiration was replaced by adding distilled water to the surface of the soil mixture. A solution of 20-20-20 soluble fertilizer (Robert Peters Co., Inc.) was used as a complete nutrient source

TABLE 1

Estimates of living shoot density (LSD), living leaf density (LLD), average maximum length of living leaves (LLL), living standing crop (LSC) and dead standing crop (DSC) and total standing leaf crops (TSC) m^{-2}, for seven different populations of *Juncus Roemerianus*. Comparison of these data shows that some populations are structurally similar while others are very different. See the map in Figure 1 for location of stations.

Population Location (Descriptive)	Station Number	Number m^{-2} LSD	cm LLD	LLL	g dry wt. m^{-2} LSC	DSC	TSC (LSC + DSC)
Bluff Creek	1	492 ± 73	886 ± 240	210 ± 30	1664 ± 210	416 ± 72	2080 ± 282
Upper Pascagoula River	2	572 ± 82	1258 ± 211	200 ± 41	2638 ± 201	465 ± 62	3104 ± 263
Lower Pascagoula River	5	782 ± 25	1715 ± 57	150 ± 10	3844 ± 150	430 ± 43	4275 ± 193
Grand Bayou	17	931 ± 21	2793 ± 44	180 ± 12	4225 ± 187	470 ± 32	4696 ± 187
Near salt flats	18	1680 ± 45	4032 ± 97	80 ± 8	1531 ± 120	1058 ± 127	2590 ± 247
On salt flats	19	170 ± 12	340 ± 20	30 ± 6	52 ± 3	14 ± 1	66 ± 4
Belle Fontaine	20	768 ± 17	1955 ± 31	215 ± 15	4196 ± 90	1632 ± 30	5730 ± 121

throughout the experiment. About 50 ml of a 5% solution was applied to the soil solution every 3 weeks. Plants were observed weekly and leaf length measured for 3 months.

All statistical comparisons used in this study are based upon analysis of variance (ANOVA).

RESULTS

Variation in Growth and Form

There is considerable variation in the vegetative growth and form of *Juncus roemerianus.* Generally, specific characteristics of growth can be associated with specific populations. Therefore, distinct populations of *J. roemerianus* can often be delineated on form, but not always. For example, there is a gradual change in leaf length, leaf density, and corresponding leaf production over a 9-mile stretch in the Pascagoula River marsh. However, if one samples the plant populations at intervals from the river mouth to the inland limit of marsh, differences in growth are obvious. Leaf length also increases near upland borders in most marshes. Kruczynski et al. (1978) states that both living and dead leaves, measured along a transect from the open water to the upland, increase away from the water. They also found that leaf length decreased towards the uplands. This situation also occurs in Mississippi, but it is found less often than the reverse relationship previously described. On areas that gradually slope from pine-dominated uplands to tidal marsh, the condition described by Kruczynski is generally found. However, where the elevation of the marsh is relatively low near the upland and abruptly changes to upland, the leaves of *J. roemerianus* are longer than those found seaward. In disjunct populations, separated by upland land masses and open bodies of water, more striking differences can be seen. Comparative data for seven different populations are shown in Table 1. These locations are represented by the numbered stations as shown in Figure 1. The plants of *J. roemerianus* tend to have longer leaves and fewer stems and leaves m^{-2} with decreasing salinity both upstream and laterally in all local estuaries. The reverse is also true with an increase in stem and leaf number (per unit of marsh surface) occurring with decreased salinity. This trend appears to be the same in the riverine populations. In a previous study, Eleuterius and Caldwell (1981) showed that the patterns and rates of growth and longevity of *J. roemerianus* varied considerably between different populations.

Vertical Distribution, Tidal Range and Evaluation

Another feature of *Juncus roemerianus* is its ability to grow over a relatively wide elevational range. Although varying from place to place, the plant species seems to be restricted to the upper half of the intertidal plane. The general elevational range of *J. roemerianus,* in relation to ranges for other important marsh species, is shown in Figure 2. Considerable overlap in ranges between these four major salt marsh species was found to occur. The comparative elevations shown for *J. roemerianus* and almost pure stands of *Distichlis spicata, Spartina alterniflora,* and *Scirpus olneyi* indicates that unknown factors related to tidal inundation and exposure are responsible for the dominance of these species at their respective elevations. Furthermore, many other plant species can occupy the same elevations also occupied by *J. roemerianus,* attested by the greater intermixture of species in brackish and very low-salinity marshes.

Edaphic Factors in General

Juncus roemerianus occurs in a wide variety of intertidal soil types. The soils range from almost pure sand to fine silt and clay mixtures and highly organic soils, including partially decomposed peat. Soils may be homogeneous, watery, unconsolidated materials (characteristic of the riverine marshes) or the more consolidated soils composed of loosely or densely compacted sand, clay, and organic material characteristic of coastal bay and bayou marshes. Some soils may be layered or zoned especially in marshes located immediately adjacent to the coast and underlying island marshes. An intensely blue clay layer often underlies these

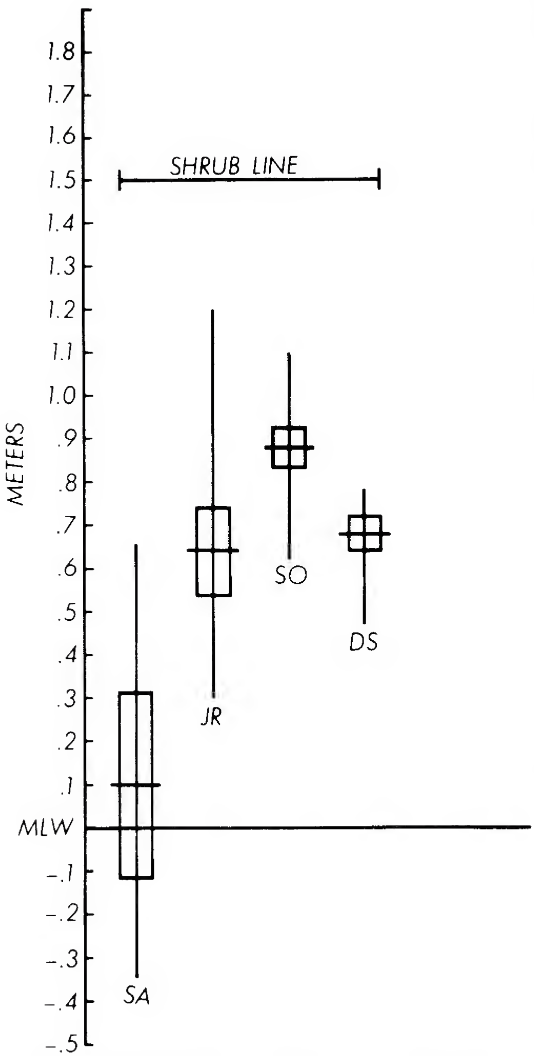


Figure 2. Elevational ranges and relationship of *Juncus roemerianus* (JR) to *Distichlis spicata* (DS), *Scirpus olneyi* (SO), *Spartina alterniflora* (SA) and mean low water (MLW).

sandy or organic surface soils. Sometimes sand is washed over organic soils in coastal and insular marshes forming layers in this fashion. *J. roemerianus* occupies a greater variety of soil types than any other marsh plant observed on the Mississippi Coast.

Soil nutrients varied considerably within and between the 26 widely separated habitats. Phosphorus (P) concentration ranged from 3 to 122 ppm, but averaged about 35 ppm in most habitats. Relatively large amounts of potassium (K) ranging from 3 to 245 ppm were found, averaging about 170 ppm for most habitats. Nitrogen (N) concentrations in many habitats were not detectable; however, in those areas where determinations were obtained, the concentrations never exceeded 3 ppm. Soil pH ranged from 4.5 to 7 with most soils having a pH of 5.8. Differences in soil composition, structure, elevation, and soil water salinity prevented any meaningful correlation between concentrations of the major plant nutrients in the soil and plant growth. Soil pH could not be correlated to plant growth for the same reasons. Furthermore, comparison of the major nutrients (NPK) found in marshes occupied by *Juncus roemerianus* with those covered by *Spartina alterniflora, Distichlis spicata, Cladium jamaicense,* and *Scirpus olneyi* showed that the nutrient concentrations of the latter fell within the range for *J. roemerianus.* All of the plant habitats examined had wide variation within and between habitats. Variability in soil structure and elevation also prevented any meaningful correlation between concentrations of the major plant nutrients in the soil. Soil pH could not be correlated for the same reason. Other factors such as seasonality, soil structure, organic matter, and soil water content also influence spatial variation. Because of the wide variation between habitats, statistically significant differences in soil nutrients or pH could be found only between some populations of *J. roemerianus.* The wide variation found within each habitat indicates a gradient between them and renders any differences in nutrient concentrations meaningless. These findings indicate that *J. roemerianus* is capable of inhabiting a wide variety of soil types with variable concentrations of nutrients.

Soil Water Salinity

Soil water availability and soil water salinity are related to tidal inundation and exposure of the marsh surface. River outflow often interrupts the general tidal patterns over riverine marshes. However, in the Pascagoula River marshes soil water salinity is cyclic and variable with season, soil depth, and location in the estuary, as shown in Figure 3A and B. Small differences occur between surface and subsurface determinations and between seasons, reflecting the general low-salinity condition which prevails in these inland marshes as shown in Figure 3A. The most inland location consistently sampled (Station 2) is least influenced by the tides and shows a low concentration and correspondingly low fluctuation in soil water salinity, while the location near the mouth of the Pascagoula River shows relatively high and low concentrations of salt at various times in the annual cycle and correspondingly wide fluctuations (Station 5 as shown in Figure 3B). The soil water salinity pattern for a station in a coastal bayou marsh (Davis Bayou, Station 15), which is strongly influenced by tidal waters, is shown in Figure 3C. This pattern is similar to that found near the mouth of the Pascagoula River, but characterized by greater concentrations and fluctuations in salinity. Relatively large differences were found between surface and subsurface determinations and seasonal determinations

indicating (Figure 3C) that considerable fluctuation occurs in this marsh (Station 15).

The greatest soil water salinity occurs on sandy "salt flats." Salinities here (Station 19) were much greater than those found in other marsh locations, but the pattern of fluctuation between surface and subsurface determinations and the general seasonal changes were similar. The wet sandy "salt flats" are apparently an amplification of salinity cycles and processes which take place throughout local tidal marshes. The soil water salinity pattern for *Juncus roemerianus* marsh areas along the edge of these "salt flats" is shown in Figure 3D. Three important facts are evident: (1) Soil water salinity varies seasonally and is cyclic in all populations; (2) the soil water salinities of the lowest depths remain the most constant; and (3) the surface layer of soil has the greatest fluctuation. The most crucial period of survival for *J. roemerianus* occurs during the summer and fall months when soil water salinity is extremely high because of evaporation and plant transpiration, especially during periods of tidal exposure in daylight hours (Eleuterius, in preparation, a).

Eleuterius and Eleuterius (1979) found that the zone of *Spartina alterniflora* in Mississippi, over an annual period, is flooded 139 times more frequently than the adjacent zone of *Juncus roemerianus* and that the duration of flooding in *S. alterniflora* was 11 times as long as that of *J. roemerianus.* Frequent tidal flooding prevents concentration of salts in the soil water, because it dilutes the soil water solution. Long periods of exposure may result in high concentration of salt, often exceeding sea strength. In many instances soil water salinity in the marsh may exceed that of the adjacent open water (bayou, bay, river, or sound). Tidal flooding also contributes to soil water salinity in those marshes under the strongest tidal influence, and when flooded by highly saline water these marshes often develop hypersaline soil water concentrations when they become exposed for long periods during summer.

Salinity, Tolerance and the Effect on Plant Growth and Form

The gradient series composed of a freshwater control (0 ppt) and seven different concentrations of salt (10–70 ppt) indicate that adaptation has occurred in plants composing some populations in the tidal marshes of Mississippi.

The salt tolerance of plants from different populations and the effect of salt on the growth of the rush can be seen by comparison of the increase in leaf length of immature plants grown in soil solutions of different salt

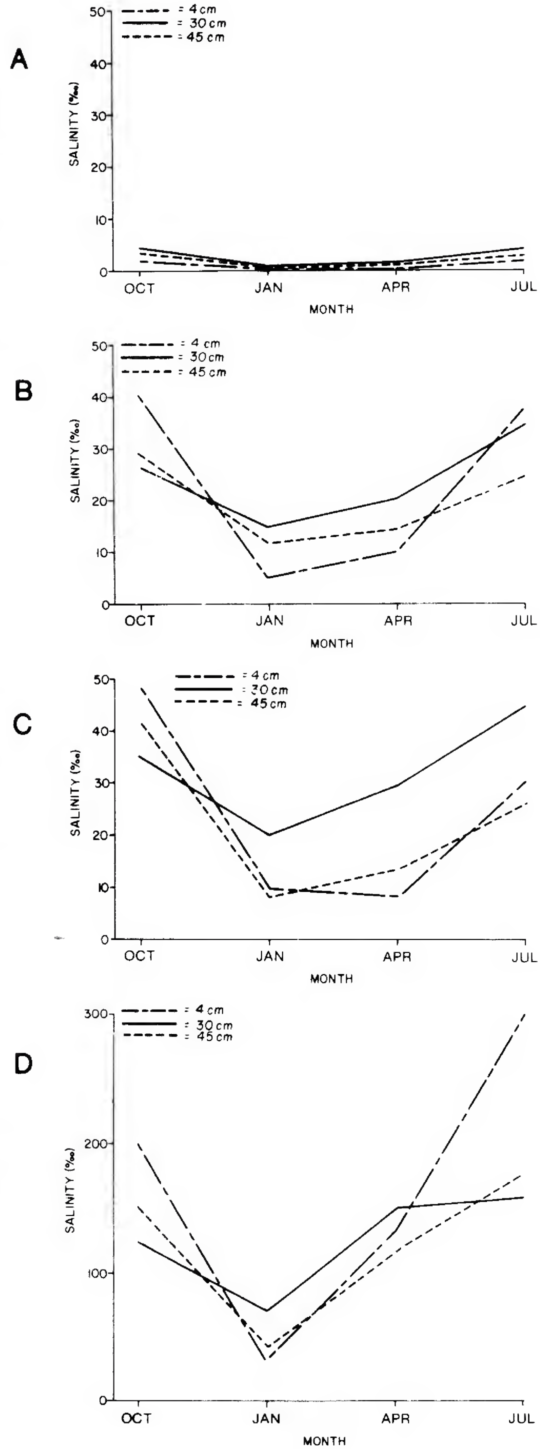


Figure 3. A. Soil water salinity as determined from soil cores from the Pascagoula River marsh near the inland limit of distribution of *Juncus roemerianus* (Station 2). B. Soil water salinity of a dense stand of *Juncus roemerianus* near the mouth of the Pascagoula River (Station 5). C. Soil water salinity of a dense stand of *Juncus roemerianus* on Marsh Point south of Davis Bay (Station 15). D. Soil water salinity of a population of *Juncus roemerianus* located on a "salt flat" on Deer Island (Station 19).

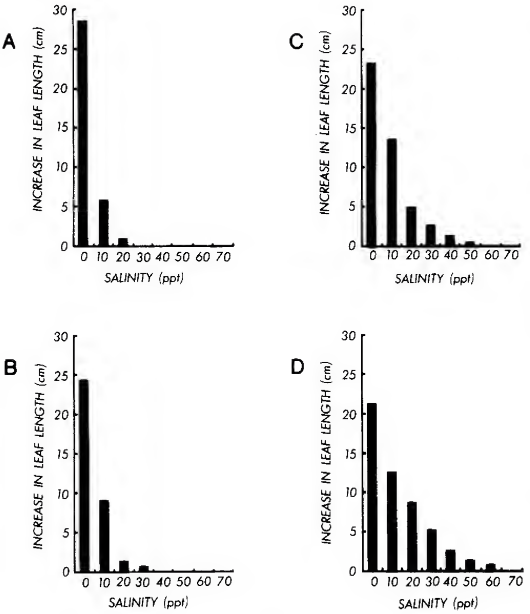


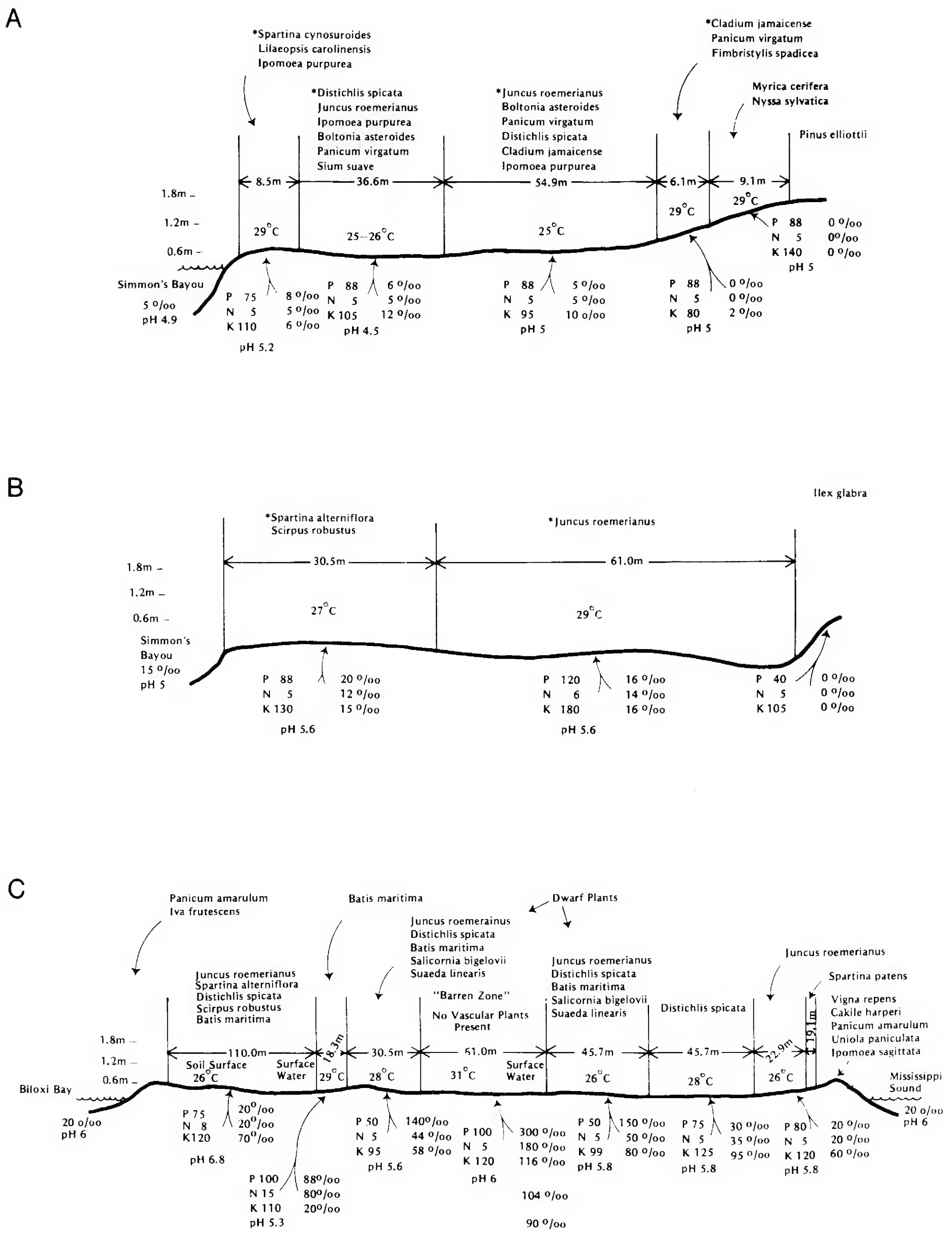
Figure 4. Growth of *Juncus roemerianus* under different salinity regimes.

concentrations for a period of 3 months. The total leaf length of the test seedlings was about 25 cm, based on measurements of all leaves present at the start of the experiment. Seedlings were selected with five leaves and leaves of similar length. An increase in the number of new leaves produced by each plant corresponds with a decrease in salinity. Transplants from the low-salinity area (Station 2) died in the highest salinities at the end of 2 weeks (Figure 4A), while others from Station 5 and Station 15 had a greater tolerance and survived a longer period of time in the higher concentrations of salt. Dwarfed transplants from the hypersaline salt flats (Station 19) exhibit the greatest tolerance (Figure 4D). The growth of all surviving transplants regardless of marsh location is decreased with increasing salinity. Survival of mature plants of *J. roemerianus* in the marsh probably occurs through two processes. One process concerns the "duration" or the length of the period of time that the plants are exposed to high salt concentration. In most populations of *J. roemerianus,* nearest the coast, relatively high concentrations of salt in soil water is not continuous. Therefore, *J. roemerianus* is able to survive these relatively "brief" periods of intense salt concentration. The second process concerns a peculiar biological attribute of *J. roemerianus.* Two kinds of roots are generally produced by *J. roemerianus* (Eleuterius 1976b). In hypersaline marshes, specialized, deeply penetrating roots (6 to 8 feet) may allow the plants to draw less saline water which occurs at lower depths. The absence of fibrous, absorbing roots produced on plant shoots near the soil surface may indicate that high concentrations of salt in the upper soil layers inhibits their formation. However, *J. roemerianus* appears to have a much greater tolerance to salt than most plants inhabiting brackish or saline marshes.

Profile Diagrams

The profiles shown in Figure 5 diagrammatically show the elevation, edaphic characteristics, plants, and plant assemblages associated with *Juncus roemerianus* taken on three subsequent days during midsummer at three different estuarine locations. These illustrations simultaneously summarize several segments of new information. Relationships between habitats of *J. roemerianus* and adjacent ones occupied by other plant species, can be readily shown from these profile diagrams by comparing plant zones, and distance and ecological, especially edaphic, data. Plant community composition and plant zonation of pure stands in low- and high-salinity regimes in the Davis Bay estuarine system are shown in Figure 5A and 5B, respectively. Some differences are found in available soil nitrogen, phosphorus, and potassium between zones or habitats at each location or between locations. Statistically significant differences are found between some zones while no differences are found between others. Substantial differences in soil water salinity were found between some zones. The soil water salinity of "salt flats" is significantly different from that of all other vegetational zones. Soil pH is significantly higher in the more saline areas. The very sandy (0.1 to 2.5% OM), barren "salt flat" on Deer Island (Station 19) is flanked by habitats with higher ratios of organic matter to sand ranging from 0.4 to 6.0% (Figure 5C). These insular habitats are often underlain at a depth of 2 m by a stratum of blue clay. The diagrams and corresponding ecological data show that *J. roemerianus* grows in a variety of habitats and occurs closely associated with several vascular plant species known to be highly salt tolerant (see associated species listed in Figure 5C). Based on edaphic data, the sites occupied by other species on Deer Island also appear to be suitable for the growth of

Figure 5. A. Profile diagram of an inland, relatively low-salinity marsh along Simmons Bayou (Station 9) showing the vegetation composition and related edaphic conditions. Elevations are shown approximately and not to scale. Soluble nutrients (NPK) are expressed in ppm, and soil water (interstitial) salinities are shown as isohalines in ppt. B. Profile diagram of a relatively high salinity marsh, seaward of the location shown in Figure 5A, near the mouth of Simmons Bayou (Station 11). The vegetation composition and related edaphic conditions are shown. C. Profile diagram of salt marshes and related areas on the eastern portion of Deer Island (Station 19). Plant species composing the plant populations and communities are shown with corresponding edaphic data. The "barren salt flat" is devoid of vegetation. Dwarf plants occur in zones immediately adjacent to the hypersaline barren zone. Soluble plant nutrients (NPK) are expressed in ppm, while soil salinities at different depths (isohalines) are shown as ppt.


A
*Spartina cynosuroides
Lilaeopsis carolinensis
Ipomoea purpurea
*Distichlis spicata
Juncus roemerianus
Ipomoea purpurea
Boltonia asteroides
Panicum virgatum
Sium suave
*Juncus roemerianus
Boltonia asteroides
Panicum virgatum
Distichlis spicata
Cladium jamaicense
Ipomoea purpurea
*Cladium jamaicense
Panicum virgatum
Fimbristylis spadicea
Myrica cerifera
Nyssa sylvatica
Pinus elliottii
8.5m
36.6m
54.9m
6.1m
9.1m
1.8m
1.2m
0.6m
Simmon's Bayou
5 o/oo
pH 4.9
29°C
25–26°C
25°C
29°C
29°C
P 75 N 5 K 110 pH 5.2
8 o/oo 5 o/oo 6 o/oo
P 88 N 5 K 105 pH 4.5
6 o/oo 5 o/oo 12 o/oo
P 88 N 5 K 95 pH 5
5 o/oo 5 o/oo 10 o/oo
P 88 N 5 K 80 pH 5
0 o/oo 0 o/oo 2 o/oo
P 88 N 5 K 140 pH 5
0 o/oo 0o/oo 0 o/oo
B
*Spartina alterniflora
Scirpus robustus
*Juncus roemerianus
Ilex glabra
30.5m
61.0m
1.8m
1.2m
0.6m
Simmon's Bayou
15 o/oo
pH 5
27°C
29°C
P 88 N 5 K 130 pH 5.6
20 o/oo 12 o/oo 15 o/oo
P 120 N 6 K 180 pH 5.6
16 o/oo 14 o/oo 16 o/oo
P 40 N 5 K 105
0 o/oo 0 o/oo 0 o/oo
C
Panicum amarulum
Iva frutescens
Batis maritima
Dwarf Plants
Juncus roemerainus
Distichlis spicata
Batis maritima
Salicornia bigelovii
Suaeda linearis
Juncus roemerianus
Spartina alterniflora
Distichlis spicata
Scirpus robustus
Batis maritima
"Barren Zone"
No Vascular Plants Present
Juncus roemerianus
Distichlis spicata
Batis maritima
Salicornia bigelovii
Suaeda linearis
Distichlis spicata
Juncus roemerianus
Spartina patens
Vigna repens
Cakile harperi
Panicum amarulum
Uniola paniculata
Ipomoea sagittata
1.8m
1.2m
0.6m
Biloxi Bay
20 o/oo
pH 6
110.0m
18.3m
30.5m
61.0m
45.7m
45.7m
22.9m
19.1m
Soil Surface 26°C
Surface Water 29°C
28°C
31°C
Surface Water
26°C
28°C
26°C
Mississippi Sound
20 o/oo
pH 6
P 75 N 8 K120 pH 6.8
20° o/oo 20° o/oo 70° o/oo
P 100 N 15 K 110 pH 5.3
88° o/oo 80° o/oo 20° o/oo
P 50 N 5 K 95 pH 5.6
140° o/oo 44 o/oo 58 o/oo
P 100 N 5 K 120 pH 6
300 o/oo 180 o/oo 116 o/oo 104 o/oo 90 o/oo
P 50 N 5 K 99 pH 5.8
150 o/oo 50 o/oo 80 o/oo
P 75 N 5 K 125 pH 5.8
30 o/oo 35 o/oo 95 o/oo
P 80 N 5 K 120 pH 5.8
20 o/oo 20 o/oo 60 o/oo

J. roemerianus indicating that considerable overlap in habitat characteristics occurs between these species.

Attention should be drawn to the fact that mature plants of *Juncus roemerianus* exist as "dwarfs" along the edge of hypersaline "salt flats" (Figure 5C). *Distichlis spicata* also grows in a dwarf form here. The "dwarf" plants of *J. roemerianus,* which flower each spring, are also associated with the succulents *Salicornia bigelovii, Suaeda linearis,* and *Batis maritima.*

Phenotypic variation of *Juncus roemerianus* may be caused by one or more edaphic factors, elevation in relation to tidal inundation, other environmental factors, or genetic differentiation. Soil water salinity is most certainly one of the major environmental factors affecting the growth and form of *J. roemerianus.* However, phenotypic variation in *J. roemerianus* may be the result of genetic differentiation (ecotypic adaptation) because entire populations often share the same characteristics, such as leaf length, shoot density, inflorescence size, etc., but no statistically significant correlation between these plant features and edaphic factors could be found.

Other Factors Affecting Growth

Another factor affecting plant growth is the accumulation of large amounts of dead-standing plant material, that is, leaves which have died but remain upright (see DSC in Table 1). Generally in most marsh areas, this dead material is periodically swept away by tidal waters, wave action, river discharge, fire, and the high winds of hurricanes and storms. However, in many protected marshes, especially near the adjacent uplands and in the upper region of bayous, which are not under strong tidal influence, large amounts of dead-standing leaf material accumulates over several years and progressively suppresses plant growth by reducing the amount of light reaching the living leaves. Thus, this accumulation of dead leaf material detrimentally effects the growth of *Juncus roemerianus.* Grazing by nutria (*Myocastor coypus*) and sometimes muskrats (*Ondatra zibethicus*) often detrimentally affect the growth of *J. roemerianus,* because they excavate and consume the rhizomes. The upper portion of the leaves of *J. roemerianus* in brackish and saline marshes are often stripped by meadow grasshoppers: *Orchelimum fidicinium, O. concinum, Conocephalus hygrophilus, C. fasciatus, Paroxya claviliger, Orphulella olivacea, O. pelidna, Clinoncephalus elegans, Meromiria intertesta* and *Dichromorpha viridis.* The grasshoppers occur in great numbers, or swarms, composed of several species. In some years, a definite pattern of succession of grasshopper species seems to occur. However, observations over a 16-year period clearly indicates that grasshopper swarms in tidal marshes of Mississippi are generally composed of mixed species which persist throughout the warmer months of the year. These grasshoppers do not feed extensively on nor do they permanently damage *J. roemerianus.* Extensive damage to *J. roemerianus* is prevented by the presence of many thick, tough fibrous strands that run lengthwise in the leaves (Eleuterius 1976b). The large grasshopper *Romalea microptera* also occurs abundantly in marshes of *J. roemerianus,* but this insect feeds on the succulent leaves of *Sagittaria lancifolia, Pontederia cordata, Crinum americanum, Hymenocallis occidentalis,* and *Iris virginica.*

One of the most important factors limiting the distribution of *Juncus roemerianus* into freshwater habitats is the difference in numbers and kinds of soil organisms found in freshwater habitats compared to those found in brackish and saline areas. Plants of *J. roemerianus* dug out of low-salinity marshes near the limit of inland distribution always have poorly developed rhizomes. The protective rhizome scales (Eleuterius 1976b) are generally decomposed or eaten away. The rhizomes also appear blackened with ragged scale fragments. Numerous observations carried out over many years (10+) indicate that the rhizomes are also perforated with holes made by what appears to be several or more different kinds of small animals that bore into and through the rhizomes of *J. roemerianus.* Rhizome destruction by soil organisms appears to limit distribution of *J. roemerianus* inland by hindering its spread and restricting its growth to isolated clumps. Competition with *Cladium jamaicense* and other herbaceous plants and swamp trees such as cypress (*Taxodium distichum*) and black gum (*Nyssa sylvatica*) is an obvious major limiting factor in the upper regions of the bayous and rivers. In each river system on the Mississippi coast *J. roemerianus* is replaced by *C. jamaicense* or it grades into tree-covered swamps.

Seed Production and Germination

About five billion seeds are produced annually by *Juncus roemerianus* in Mississippi. Plants bearing pistillate flowers generally produce more seed than plants with perfect flowers. Light is required for germination. Seeds buried under mud or organic soil will not germinate. Seeds germinate totally submerged under clear water in the presence of light with an intensity of 2153 lux (200 foot candles) or greater. Germination is decreased with increasing salinity and inhibited by salinities above 15 ppt (Table 2). However, many of the salt-inhibited seeds, which were subsequently rinsed thoroughly in fresh water, germinated under freshwater conditions. Also, seedling growth decreased with increased salinity. Seeds from plants bearing pistillate flowers were more viable than those bearing perfect flowers. Germination of seed from pistillate flowers ranged from 24 to 100% and those from perfect flowers ranged from 0 to 96%. However, there was a significant difference between the two seed groups. Ninety-five percent (95%) of all seed samples from plants with pistillate flowers germinated within a range of 65 to 85%, with an average of 75%. Ninety-five percent (95%) of all seed samples from perfect flowers germinated within the range of 42 to 77%, with an average of 60%. Perfect flowers may be self-pollinated and the lower seed viability may represent an inbred weakness.

TABLE 2

Inhibition and germination of seeds in various concentrations of sea salt solutions at room temperature and under 360 foot candles of light. Approximately 100 seeds were placed on each plate.

Salt Concentration ppt	Percent Germination ♀	Percent Germination ♀♂	Number of days for germination to occur
Distilled water	73	52	7
1	67	47	7
2	58	36	7
5	34	20	14
7	17	11	21
10	6	2	30
15	0	0	
20	0	0	
25	0	0	
30	0	0	

Many seed samples from perfect flowers were not viable. The seeds from plants with pistillate flowers are round in cross section, full, robust, dark brown or reddish brown. However, the seeds from plants with perfect flowers are often flattened, thin, transparent, light brown, tan or yellowish in color. A few seeds in each capsule may be robust, but generally they are slightly smaller in size (Eleuterius 1975).

Seedling Establishment

A conspicuous aspect of all populations of *Juncus roemerianus* is the absence of seedlings. Perhaps the dense vegetative canopy reduces light below the required intensity for germination. Furthermore, none have been found on muddy or organic substrates, vegetated or barren, probably because the seeds are easily buried. Seedlings have been found on sand substratum. A sandy substratum probably favors germination, because sufficient light penetrates through the thin layer of sand covering the seeds and the seeds are not easily covered by sand. On sandy shores and sandy areas resulting from dredging operations, seedlings often become established, but few plants reach maturity. About 20 seedlings were observed on a sandy shore, near the high tide lines (4 feet above MLW), several years ago. About 75% were subsequently lost because of erosion from heavy rains, storm waves, and currents. Most of the seedlings were washed away, others were buried. Later, drought or salt concentrations in the soil probably caused the death of the remaining seedlings. In other instances, I have seen a few seedlings become established and develop into mature stands, but always associated with great mortality of seedlings. The seedlings of *J. roemerianus* are obviously much more sensitive to environmental stress than mature plants.

The vulnerable stages in the life cycle of *Juncus roemerianus* are, therefore, germination and seedling establishment. Once seedlings reach maturity, the rush becomes an aggressive colonizer. Mature plants of *J. roemerianus* maintain a dense stand by vigorous rhizome growth. The rate of rhizome growth is not rapid in comparison to many other tidal marsh plants, but on new terrain and in the best developed stands, the production of new rhizomes is prolific. Mature plants are steadfast, strong competitors, persistent in growth, and are therefore aggressive colonizers.

DISCUSSION

The availability of the major soluble nutrients, nitrogen (N), phosphorus (P), and potassium (K) cannot be used to delineate the habitat of *Juncus roemerianus* from that of *Spartina alterniflora, Distichlis spicata, Scirpus olneyi,* and *Cladium jamaicense.* Furthermore, NPK concentrations could not be used to separate morphologically distinct populations of *J. roemerianus.* The spatial variation of NPK within and between *J. roemerianus* populations and habitats of other plants indicates that nutrient availability is influenced by soil water salinity, season, elevation, soil structure, organic matter content (Boyd 1970), and the frequency and duration of the tides. Relatively large amounts of K and P are readily available in all tidal marsh soils sampled and certainly do not seem to be a limiting factor. Available N was not detected in most soil samples. However, N transformation in wetland soils and the effect on the vegetation has been the subject of intensive research (Waring and Bremner 1964, Tyler 1967, Maye 1972, Ponnaperuma 1972, Engler and Patrick 1974, Delaune, et al. 1976). How *J. roemerianus* and many other tidal marsh plants obtain a sufficient supply of N remains, at present, unknown. Researchers have recently shown that some aquatic plants are capable of nitrogen fixation (Patriquin and Knowles 1972). However, it should be pointed out that the distribution of other soil nutrients, such as sulfur, iron, cobalt, zinc, and magnesium, may differ significantly between populations of *J. roemerianus* and those of other marsh plants. I conclude this section on soil nutrition by pointing out that in the inland, low-salinity regions of tidal marshes in Mississippi, more than 50 species of plants occupy the same wetland terrain as *J. roemerianus* (Eleuterius 1972, Eleuterius and McDaniel 1978, and Eleuterius 1980b). These species occur intermixed with *J. roemerianus* at the same elevation, soil structure and nutrient concentration. Because of their abundance, the major soil elements utilized as nutrients by *J. roemerianus,* do not seem to be a limiting factor for the growth and distribution of the rush. The amount of water composing a soil sample is a nebulous measurement because of the ebb and flood of the tide and fluctuation caused by evaporation. However, the amount of water composing the solution is important in relation to the concentration of soil nutrients. Thus, the concentration of plant nutrients in the soil solution is obviously in a constant state of fluctuation. This may account for the difficulty in relating plant growth to nutrient concentrations in soil solutions in tidal marshes. Ho (1971) found that seasonal changes occurred in the water and sediment of an estuary in Louisiana. The

soil data obtained in the present study compare favorably with those of marshes found in Louisiana, Florida, and Georgia (Chabreck 1972, Maye 1972, Stewart, et al. 1973, Burpbacher, et al. 1973, Volk, et al. 1975, and Steward and Ornes 1975). It is concluded that *J. roemerianus* is capable of inhabitating a variety of soil types with different nutrient concentrations.

Elevation is an important factor in the seaward distribution of *Juncus roemerianus. Spartina alterniflora* can tolerate considerably more tidal flooding in comparison to *J. roemerianus* which is clearly shown in the present study and by previous research (Kurz and Wagner 1957, Adams 1963, Eleuterius and Eleuterius 1979). *J. roemerianus* has a wide vertical range above mean low water, which means that it grows at the same elevation as many other tidal marsh plants. In the lower regions of riverine marshes where tidal influence is greatest, *J. roemerianus* grows at the same elevation as almost pure stands of *Distichlis spicata* and *Scirpus olneyi,* and in some places at the same elevations as almost monotypic stands of *Spartina alterniflora, Spartina patens, Spartina cynosuroides,* and *Cladium jamaicense.* In the inland, low-salinity riverine regions, *J. roemerianus* occurs, as stated above, at the same elevation as 50+ species of tidal marsh plants. Therefore, elevation, per se, can not delineate individual populations or the overall habitat of *J. roemerianus* from that of many other plants. Eleuterius and Eleuterius (1979) showed that other factors are obviously involved in delineating a habitat of *J. roemerianus* from *Spartina alterniflora,* but the factors were not defined. *J. roemerianus* was shown to occupy the upper 40% of the intertidal plane in an estuarine marsh strongly influenced by the tide at a single location in Mississippi.

Competition with other flowering plants is an important factor in the distribution of *Juncus roemerianus.* The leaves become longer, but shoot density decreases as the number of competitor plants increases upstream and inland in riverine marshes and in the upper ends of bayous strongly influenced by the tides. Penfound and Hathaway (1938), O'Neal (1949), and Gillham (1957) reported similar distributional patterns. The overall effect of competition is a reduction in growth and production of the rush. Plants representing the limit of inland distribution are also in competition with an array of microflora not found in the more saline downstream marshes.

Plant zones in hypersaline areas appear almost stabilized, based on observations over a number of years. Invasion of a zone by plants from an adjacent zone does not readily occur. The plant zones appear to represent plant populations in a state of balanced existence unique to tidal marshes.

Soil water salinity is the most important factor affecting the growth and distribution of *Juncus roemerianus.* Salinity was also determined to be the major factor affecting plant zonation in tidal marshes by Reed (1947), Jackson (1952), Kurz and Wagner (1957), and Adams (1963). Soil water salinity operates in two ways to favor the growth of *J. roemerianus.* One way is the removal of competing flowering plants, which are less salt tolerant than *J. roemerianus.* Death of less salt tolerant competitors favors the growth and spread of *J. roemerianus* by providing more space and reducing competition for nutrients and light. Soil water salinity reaches annual peaks in August and October. Observations made over a number of years indicate that the August peak may be modified by heavy summer rains, but the October peak has consistently occurred locally without interruption for the past decade. Therefore, the greatest upstream penetration and effect of salt water in bayous and rivers occurs during October and early November of each year. This relatively brief period (3 to 6 weeks) of salt water intrusion also benefits *J. roemerianus* by the modifying effect on the soil microorganisms. The introduction of salt into the soils of these otherwise freshwater-dominated tidal marshes obviously kills or reduces the number of harmful microorganisms (Eleuterius, in preparation, b). Thus, tidal influence also delineates salt marshes on an areal basis by the direct introduction of sea salt into the soil solution. In Mississippi, the tidal amplitude is relatively small with an 1.8 foot range between high and low tides. However, the annual cycle of highs and lows may extend over a vertical range of 5 feet or more (Eleuterius and Eleuterius 1979). Therefore, seasonal patterns of tides are important and represent a complex relationship to plant distribution (Chapman 1976). *J. roemerianus* extends 10–15 miles inland along the river estuaries. A similar pattern is also found in coastal bayous, where the number of associated species increases with decreased salinity. In Mississippi, the rush dominates 92% or about 25,000 hectares of tidal marsh (Eleuterius 1972). This extensive coverage also suggests that the rush has relatively wide environmental tolerances.

Soil water salinity has pronounced effects on the growth, form, and the physiological adaptation of *Juncus roemerianus* and also inhibits germination. Phlegher (1971) also found that salt concentration in sand cultures reduced the growth of *Spartina foliosa* Trin. In the present study, where the entire root mass was included in the test container and the salinity of the soil water remained constant, the test plants from different populations were shown to have different tolerances to salt, but each test group had definite limits to their ability to withstand high concentrations of salt. These data indicate that different populations of *J. roemerianus* have different tolerances to salt. Furthermore they strongly suggest that physiological adaptation has occurred in the different populations studied. In nature, however, soil water salinity fluctuates and the soil water salinity decreases with increasing depth. The hypersaline soil water regime found on the salt flats appears to be an amplification or an exaggeration of the same process that takes place in other habitats of *J. roemerianus.*

Comparison of the effects of salinity on germination with tolerances of mature plants indicates that tolerance to

salt obviously increases with maturity. Absence of seedlings in vegetated tidal marshes may also result from the failure of seed to germinate, because the seeds are quickly buried in muddy substratum, or they become coated with fine mud particles, where without the presence of light they can not germinate, or they are simply swept out to sea. Richards and Clapham (1941), Lazenby (1955), Tadmor, et al. (1958), and Welch (1966, 1967) found that other species of *Juncus* required light for germination. Furthermore, the low ambient temperature of winter and more frequent rainfalls indirectly result in lower soil water salinity and reduce stresses on *J. roemerianus.* Low temperatures reduce evaporation and transpiration. The low temperatures and low-salinity regimes of winter favor germination and seedling growth.

Chapman (1942) presented data on the germination of *Juncus maritimus* after 23 days in tap water and various concentrations of salt. Germination in tap water was 50%, 10 ppt–18%, 20 ppt–5%, and 33 ppt–0%. He also showed that germination of an unidentified species of *Salicornia* was reduced with increased salinity, but 12% germination occurred in 100 ppt NaCl. Ungar (1962) indicated that the limiting factor for seed germination of *Salicornia* under high salinities was chiefly osmotic. This appears to be true also for *J. roemerianus.* Ayers (1951) also reported a steady drop in *Salicornia* germination with increased salinity. Ungar (1962) reported an abrupt decrease in *Salicornia* germination when a 50 ppt salt concentration was reached. The retardation and prevention of germination of *J. roemerianus* by high salinity in the present study is obviously caused by osmotic factors.

Salinity is known to affect many aspects of the metabolism of plants and to induce changes in their anatomy and morphology (Uphof 1941, Bernstein and Hayward 1958, Nestler 1977). These changes are often considered to be adaptations which increase the chances of the plant to endure stress imposed by salinity (Waisel 1972, Poljakoff-Mayber and Gale 1975). Numerous investigations into the constitution of various species of plants from different ecological groups showed that only a few phenotypical adaptations, such as ecads, actually exist. Most of the populations investigated went through the action of natural selection to form genetically fixed ecotypes (Turesson 1922, 1931, Stebbins 1950, Waisel 1959). Salt-resistant forms have evolved in *Typha angustifolia* L. and *T. latifolia* L. in soil containing high concentrations of salt (McMillan 1959, McNaughton 1966). Similar results were obtained for *Phragmites communis* Trin. (Waisel 1972). In order for evolutionary change to occur, there must be a source of genetic variation and a driving force (Grant 1971, Jones and Luchsinger 1977).

Soil water salinity appears to exert a selective pressure on *Juncus roemerianus,* which has resulted in physiological and perhaps genetic differentiation. Physiological and genetic variation may account, in part, for the phenotypic variation between different populations of *J. roemerianus.* Paradoxically, the absence of seedlings in the marsh does not provide the number of progeny of different genotypes upon which a selective force, such as soil water salinity, can work. This conflict in operative mechanisms may be deceptive since the selective process is a slow one which may have occurred ages ago. Corroborative support for this possibility is the present maintenance of the mature stands of *J. roemerianus* by vigorous vegetative growth for long periods of time. These results and interpretations have evolutionary implications and raise important questions regarding the future survival of *J. roemerianus.*

Other factors affecting the growth of *Juncus roemerianus,* described in this study, are of minor importance. However, I should point out in closing this discussion that there looms on the horizon a greater threat to survival of *J. roemerianus* and all other components of tidal marshes, both plant and animal. Although both federal and state agencies are charged with the responsibility to safeguard our estuaries and tidal marshes, domestic and other forms of pollution continue unabated, and estuarine water quality continues to decline. A continuation of this trend may have a severe effect on the future of *J. roemerianus* and other estuarine organisms well adapted to relatively pristine environments.

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A Review of the Genus Clythrocerus (Brachyura: Dorippidae) in the Eastern Gulf of Mexico with Notes on *Clythrocerus stimpsoni*

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A REVIEW OF THE GENUS *CLYTHROCERUS* (BRACHYURA: DORIPPIDAE) IN THE EASTERN GULF OF MEXICO WITH NOTES ON *CLYTHROCERUS STIMPSONI*

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ABSTRACT The four members of the dorippid crab genus *Clythrocerus* from the Gulf of Mexico are reviewed. The rediscovery of *C. stimpsoni* has allowed for the first description of the male of the species. Known previously only from the unique holotypic female, the rediscovery of *C. stimpsoni* is based on material from the same general area as the type-locality. *Clythrocerus granulatus* and *C. perpusillus* are reported for the first time from the Gulf of Mexico. The latter form was the most frequently collected species of *Clythrocerus* from the study area. Although no specimens of *C. nitidus* occurred in our samples, previous records from the Gulf of Mexico are reviewed and the species is figured from supplemental material. Available sediment data are given for the species and male gonopods are figured.

INTRODUCTION

The unusual dorippid crab genus *Clythrocerus* A. Milne-Edwards and Bouvier, 1899, is represented by four nominal species in the northwestern Atlantic (Rathbun 1937). Of these four taxa only two species, *C. stimpsoni* Rathbun, 1937, and *C. nitidus* A. Milne-Edwards, 1880, have been reported previously from the Gulf of Mexico. Rathbun (1937) described *C. stimpsoni* from a single female taken off the west coast of Florida and the Gulf record for *C. nitidus* is based on an immature specimen collected south of Cape San Blas, Florida.

MATERIALS AND METHODS

Material examined during this study came primarily from recent collections made by the Minerals Management Service (formerly the Bureau of Land Management) on the carbonate shelf of west Florida. Specimens were collected with box cores at depths ranging from 10 to 189 m. Supplemental material was examined from the National Museum of Natural History. Representative series of the species from our material have been deposited in that institution.

RESULTS

Dorippidae De Haan, 1841

Clythrocerus A. Milne-Edwards and Bouvier, 1899

Diagnosis — Carapace usually flattened, rounded; first three abdominal segments visible in dorsal view; orbits incomplete; 5th pair of legs dorsal in position; external maxillipeds elongate and covering buccal cavern; efferent orifices continuous, united in a gutter approaching frontal border; no afferent opening at base of anterior pereopods; antennules small and rectractile; antennae very short with valviform peduncle; exopods of 2nd and 3rd maxillipeds rudimentary (modified from Rathbun 1937).

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Clythrocerus stimpsoni Rathbun, 1937
(Figure 1)

Clythrocerus stimpsoni Rathbun, 1937; 121, fig. 32, pl. 34, figs. 5 and 6.

Diagnosis — Carapace convex; anterior teeth of carapace separate from remainder of carapace by depression; 2 large lateral teeth at widest part of carapace and smaller anteriorly directed tooth above margin; surface granulate with lateral margins spinulose; rostral tooth more advanced than preorbital teeth; oblique spinuliferous ridge on merus of maxilliped; pterygostomian ridge armed with spines and extending to a point opposite 1st lateral tooth of carapace.

Material examined — 1♂, 29°35′00″N, 87°20′02″W, November 1977, 106 m, coarse sand; 1♀, 29°42′59″N, 86°15′30″W, 6 June 1974, 67 m, medium sand; 1♂, 26°24′57″N, 84°15′00″W, 9 August 1977; 2♂♂, 2♀♀ (1 ovig), 26°24′57″N, 84°15′00″W, November 1977, 168 m, silty very fine sand; 1 ♀ (ovig), 25°40′00″N, 84°15′00″W, November 1977, 180 m, silty very fine sand; 1♀, 25°40′00″N, 83°50′00″W, 9 August 1977, 120 m, medium fine sand; 1♂, 26°16′45″N, 83°47′45″W, 22 July 1981, 89 m, coarse sand; 1♂, 26°16′45″N, 83°47′45″W, 30 April 1981, 90 m, fine sand; 1♂, 26°16′00″N, 84°15′00″W, 25 July 1981, 180 m, medium sand; 2♀♀ (1 ovig), 25°15′00″N, 84°15′00″W, 2 August 1981, 180 m, medium sand.

Description of male — Male very similar to female, differing in following aspects; smaller than female with branchial tubercles fewer in number; accessory spinules of lateral spines of carapace well developed, but not as numerous as in female; carapace as long as broad; abdominal segments 4–7 fused with medial and lateral elevations evident on somites 1–3; gonopod as illustrated (figure 1).

Chelipeds of female heavy, spinose; merus stout, inflated with few anterior spinules at midlength and posterior at base; palm inflated with few large spines, fingers narrow with large spines on dorsal surface of fixed finger; movable finger with spines on outer face with small tubercles proximally on dactyl.

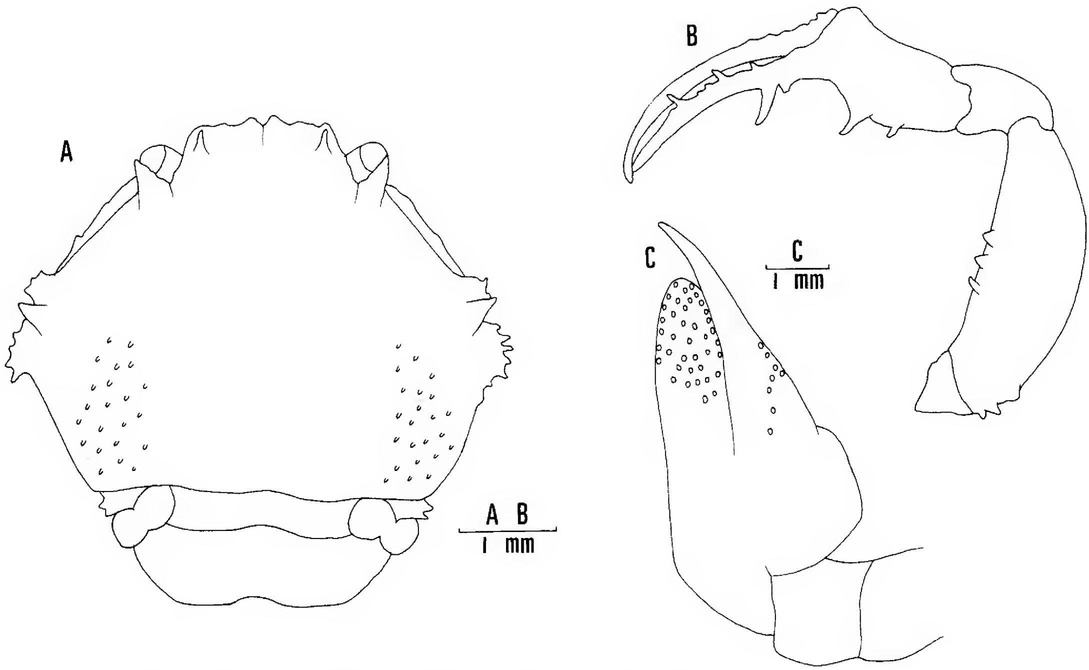

Figure 1. *Clythrocerus stimpsoni.* A. Female, legs removed; B. Male, cheliped outer face; C. Male, gonopod one.

Remarks – *Clythrocerus stimpsoni* was described by Rathbun (1937) from a single specimen collected off the west coast of Florida in 1872 by W. Stimpson. This report is the first subsequent record of this taxon and has made the description of the male possible with notes on variation and ecology. The material on which this study is based agrees closely with the original description of Rathbun (1937:121) with the exception of the following minor points: (1) Rathbun describes and figures a medial rostral tooth on the type specimen. Our specimens possess 2 rostral teeth, closely approximated medially; (2) our material has only branchial regions with numerous large tubercles, whereas Rathbun reports "surface finely granulate, a few larger tubercles in advance" (1937:121); (3) the large teeth of the lateral margins with large, well-defined spines, not "minute spinules"; (4) pterygostomial ridge of largest specimens armed with 12 to 15 spinules; and (5) a large superior lateral tooth. The variance exhibited in these characters is relatively minor and within the range for natural variation when considering the size differences and sexual maturity of available material.

No ecological data was presented with the description. The range for this species may now be expanded to cover the entire west coast of Florida, from south of Mobile Bay to northwest of the Dry Tortugas in 67 to 180 m of water. Collection data indicate substrata of coarse sand to silty, very fine sand composed primarily of carbonates.

Clythrocerus granulatus (Rathbun, 1898)
(Figure 2)

Cyclodorippe granulata Rathbun, 1898:293, pl. 9, fig. 1.
Clythrocerus granulatus: Rathbun, 1937:119, text-fig. 31, pl. 33, figs. 5–8; Williams, McCloskey and Gray, 1968: 45, fig. 3.

Diagnosis – Single dorsolateral tooth at widest part of carapace; carapace and appendages densely granulate, margins of carapace spinuliferous in posterior 1/2; interorbital region with teeth; rostral and orbital region depressed with remainder of carapace little inflated; pterygostomial region with deep furrow. Carapace slightly broader than long.

Material examined – 1 ♀ (ovig), 28°49′59″N, 85°37′02″W, November 1977, 175 m, clayey, sandy silt; 1 ♀ (ovig), 27°57′00″N, 84°47′59″W, September 1977, 189 m, silty, very fine sand; 1 ♀ (ovig), 26°45′00″N, 84°15′00″W, 17 July 1981, 170 m, medium sand; 2 ♂♂, 2 juveniles, 25°45′00″N, 83°59′00″W, 27 July 1981, 170 m, medium sand.

Remarks – Our records constitute the first reported occurrence of *C. granulatus* from the Gulf of Mexico. *Clythrocerus granulatus* is a distinctive little crab ranging from North Carolina, Florida and the type-locality of Trinidad

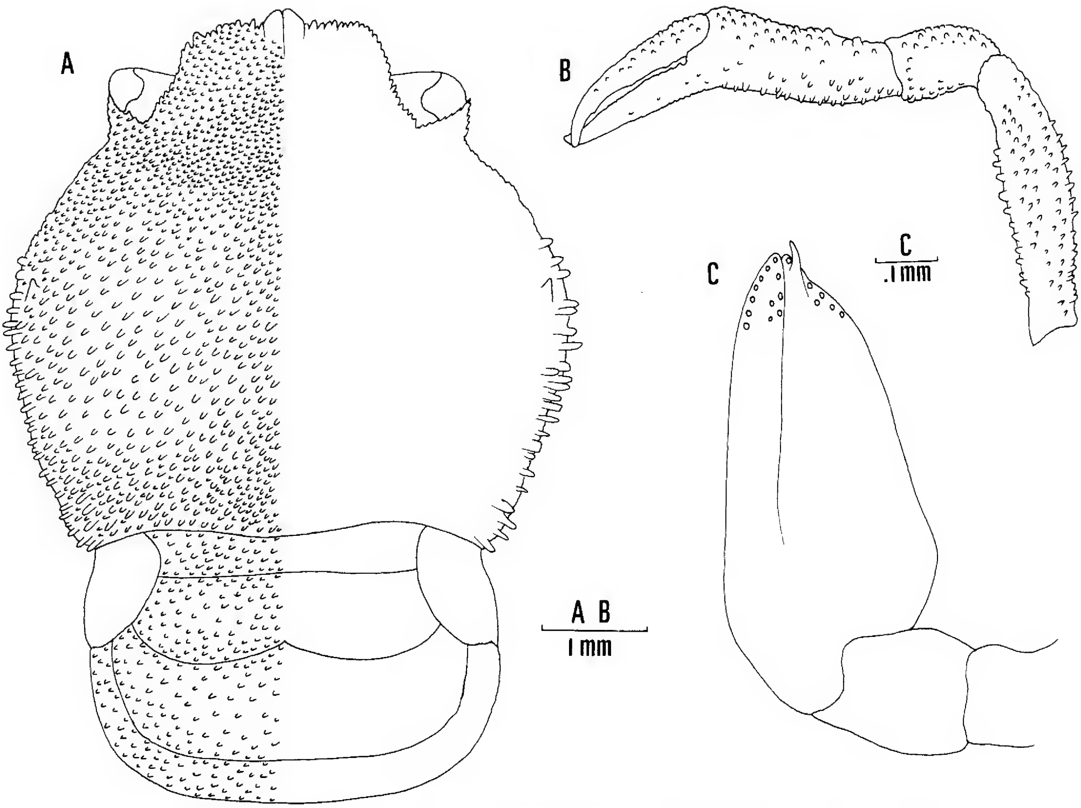

Figure 2. ***Clythrocerus granulatus.*** **A. Female, legs removed; B. Male, cheliped outer face; C. Male, gonopod one.**

to Venezuela, in waters as deep as 567 m. In the Gulf of Mexico this species has been collected along the west coast of Florida as shallow as 29 m. Material from the eastern Gulf agrees well with descriptions of Rathbun (1937). Our specimens were collected on substrata of clayey, sandy silt and medium coarse sand of carbonate origin.

Clythrocerus perpusillus **Rathbun, 1901**
Figure 3

Clythrocerus perpusillus Rathbun, 1901:90, fig. 14; Rathbun, 1937:111, text-fig. 28, pl. 33, figs. 3 and 4; Williams, McCloskey and Gray, 1968:44.

Diagnosis – Carapace flat, very finely granulate, slightly broader than long; a single tooth at widest part of carapace on margin, margins sometimes pubescent; a slight indentation in margin of carapace in front of lateral teeth.

Material examined – 3 ♂♂, 10 ♀♀, 28°38′00″N, 97°20′00″W, 90 m, 27 May 1979, coarse sand; 1 ♂, 27°37.2′00″N, 83°53.5′00″W, 50 m, 9 August 1977, coarse sand; 1 ♂, 26°24′56.8″N, 84°15′00″W, 168 m, 9 August 1977, silty fine sand; 1 ♂, 28°49′59.1″N, 85°37′01.9″W, 175 m, August 1977, clayey, sandy silt; 1 ♂, 29°42′59.9″N, 85°15′28.6″W, 67 m, February 1977, coarse sand; 1 ♂, 27°56′29.5″N, 83°52′59.5″W, 43 m, February 1977, coarse sand.

Remarks – This material represents the first reported occurrence of *C. perpusillus* in the Gulf of Mexico where it was the most commonly occurring species of *Clythrocerus* collected in our study. Specimens were examined from south Florida to the DeSoto Canyon in the northeastern Gulf. In the western Atlantic this species has been reported from the type-locality of Puerto Rico, Barbados, and North Carolina; in depths of 27–175 m. Our material occurred in depths of 43 to 175 m on substrata composed of clayey silt to coarse sand. All specimens from the Gulf of Mexico fit the description of Rathbun (1937) except for lack of lateral marginal pubescence on our specimens.

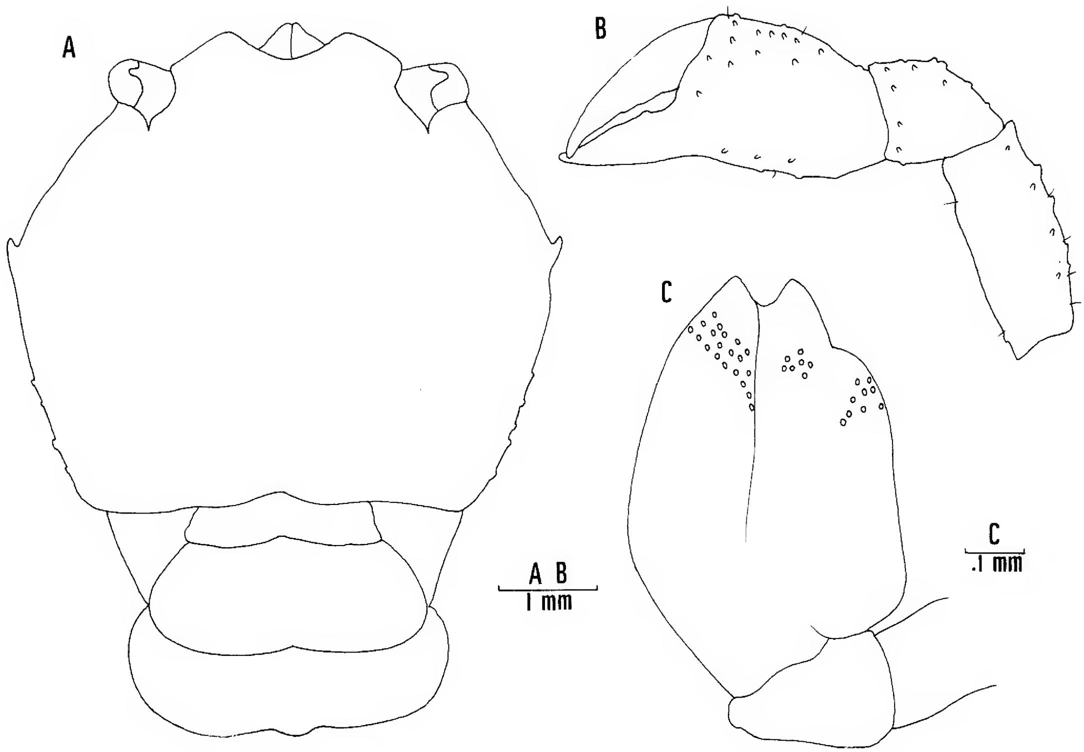

Figure 3. *Clythrocerus perpusillus.* A. Female, legs removed; B. Male, cheliped outer face; C. Male, gonopod one.

***Clythrocerus nitidus* (A. Milne-Edwards, 1880)**
Figure 4

Cyclodorippe nitida A. Milne-Edwards, 1880:24.
Clythrocerus nitidus: A. Milne-Edwards and Bouvier, 1902:90, pl. 18; Rathbun, 1937:109, text-figs. 26, 27, pl. 33, figs. 1, 2; Wass, 1955:170; Powers, 1978:26.

Diagnosis – Carapace slightly oval from side to side, carapace smooth, single supramarginal lateral tooth, no rostral teeth, branchial sutures distinct.

Material examined – USNM 66843, 16 ♂♂, 18 ♀♀ (11 ovig), 16 June 1893, off Sand Key, Florida, 219 m.

Remarks – No specimens of *Clythrocerus nitidus* were collected during this study although previous records include South Carolina, the type-localities of the Florida Keys and Grenada and northwest Florida in depths of 12–479 m. Wass (1955:170) reported this species as "known or expected to occur" from an area southwest of Cape San Blas. That report was based on Rathbun's (1937) examination of an ALBATROSS specimen collected 7 February 1885 (USNM 19878). No sediment data was given for that specimen but others are reported from rocky bottoms, coral, sand, and soft coral ooze. Material figured for this report was collected from the southeast Atlantic coast of Florida.

Discussion – Rathbun (1937:109) reported seven members of the genus *Clythrocerus* from the east and west coasts of middle America. This genus is a group of comparatively small crabs (often <5 mm) which may be confused with the closely related genus *Cyclodorippe* A. Milne-Edwards, 1880. This latter genus is represented by two nominal species in the western Atlantic and is separated from *Clythrocerus* by elongate antennules and antennae with a narrow peduncle. The broad range of variation in selected morphological features (i.e. gonopods, carapace spination) within the genus *Clythrocerus* may reflect a polyphyletic origin of the group. The establishment of new generic or subgeneric levels must accompany a review of the group as a whole and is beyond the scope of this contribution.

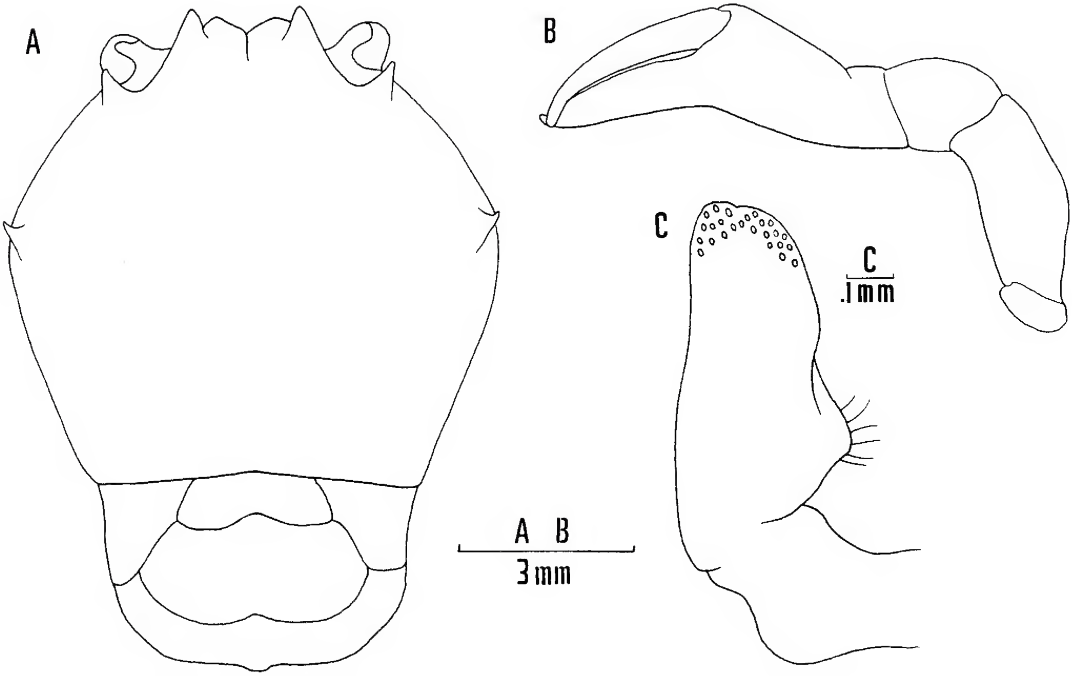

Figure 4. ***Clythrocerus nitidus.*** **A. Female, legs removed; B. Female, cheliped outer face; C. Male, gonopod one.**

PRELIMINARY KEY TO THE GENUS *CLYTHROCERUS* IN THE WESTERN ATLANTIC

1. Lateral margins of carapace unarmed except for single tooth at widest part 2
   Lateral margins of carapace with tooth at widest part above margins and with spinules or additional teeth 3
2. Carapace smooth, shiny, convex from side to side; pseudorostrum not developed forward; interocular teeth acute . . . . *Clythrocerus nitidus*
   Carapace finely granulate, flat; pseudorostrum developed beyond frontal teeth; interocular teeth blunt . . . . *Clythrocerus perpusillus*
3. Surface of carapace densely covered by coarse granules, single large lateral tooth with most accessory spinules in posterior half of margins of carapace . . . . *Clythrocerus granulatus*
   Surface of carapace finely granulate, 3 lateral teeth with accessory spinules on the 2 marginals. . . . . *Clythrocerus stimpsoni*

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GROWTH AND PRODUCTION OF THE DWARF SURF CLAM *MULINIA LATERALIS* (SAY 1822) IN A GEORGIA ESTUARY

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ABSTRACT The bivalve *Mulinia lateralis* is a dominant member of estuarine benthos, but its presence and abundance in Georgia estuarine waters is sporadic over time. Recruitment and production was monitored from 1977 through 1981 at three inner and one outer more saline (> 18 ppt) areas of Wassaw Sound. Until the winter of 1981, *Mulinia lateralis* was absent or at very low densities. Significant settlement occurred in January 1981 when densities in the outer sound reached as high as 63,000 individuals $\cdot$ m^{-2}. The clam was more abundant in sandy mud ($\bar{x}$ = 10,161 $\cdot$ m^{-2}) than mud ($\bar{x}$ = 277 $\cdot$ m^{-2}) or sand ($\bar{x}$ = 263 $\cdot$ m^{-2}). Cohort production varied from 0.3 g dry wt $\cdot$ m^{-2} $\cdot$ 4 months^{-1} in the inner sound to 325 g dry wt $\cdot$ m^{-2} $\cdot$ 7 months^{-1} in the outer Sound, with the mean biomass ranging from 0.6 to 513 g dry wt $\cdot$ m^{-2}, respectively. When present, *Mulinia lateralis* contributes significantly to benthic production available to commercially valuable fish and crabs. That this food resource is annually and seasonally episodic could contribute to year-to-year fluctuations in production of species preying on benthos.

INTRODUCTION

The dwarf surf clam *Mulinia lateralis* (Say 1822) (Bivalvia; Mactridae) is a typical dominant member of estuarine benthos whose density characteristically fluctuates widely. Populations of this clam may dominate the benthos one year or part of a year, only to be absent the following year(s). Fluctuations in the abundance of benthos of Wassaw Sound, in Georgia (Fig. 1), may be in part caused by salinity depressions in winter/spring when many benthic species spawn (Walker et al. 1980, Walker and Tenore 1984). For example, *M. lateralis* and the northern hard clam *Mercenaria mercenaria* (Linné) did not settle significantly between 1977 and 1980, when low winter salinities resulted from heavy rainfall in upstate Georgia. Because of a drought in 1981, salinities were not depressed in winter/spring and a significant set of juveniles of *M. mercenaria* and *M. lateralis* occurred.

The contribution of *M. lateralis* to benthic production is especially important because this species, when present, is an important source of food for many commercially valuable fish and crabs (Brever 1957, Tagatz 1969, Virnstein 1977). Little information exists on the production of opportunistic species such as *M. lateralis*. We describe here the production of a single cohort age-class of *M. lateralis* following the 1981 set of this bivalve after several years of recruitment failure. Information was gained on the contribution of the clam to benthic production during a period of high clam density.

STUDY SITE

Wassaw Sound (Fig. 1) is a coastal estuarine embayment located in the Georgia Bight (Howard and Frey 1980). Semidiurnal tides average 2.4 m, with spring tides ranging approximately 3.4 m (Hubbard et al. 1979). Water temperatures (Dörjes 1972) and salinities at the mouth of the Sound (Howard and Frey 1980) range from 8°C and 20 ppt in the winter to 30°C and 30 ppt in the summer. Sediments range from silt-clay to fine sand with interbedded sand and mud the most prevalent (Howard and Frey 1975).

MATERIALS AND METHODS

Four stations (Fig. 1) were sampled monthly from January to December 1981 by taking six 0.05-m^2 van Veen grabs at each station. Samples were sieved through a 0.297-mm mesh and preserved in 10% formalin in sea water. Samples were returned to the laboratory, sorted under a dissecting scope and specimens of *M. lateralis* were counted and measured for shell length (longest possible measurement, i.e., anterior-posterior distance).

Station 1 was located in the Skidaway River approximately 1 mile south of the Skidaway Institute of Oceanography where the clams occurred in a muddy substrate in approximately 1.5 m of water at mean low water. Station 2 was located in the Wilmington River at the U.S. 80 drawbridge at Thunderbolt, Ga., where the clams occurred in a muddy substrate in approximately 0.5 m of water at mean low water. Station 3 was located at the junction of Skidaway and Wilmington rivers, where the clams occurred in a sandy mud substrate in approximately 2 m of water at mean low water. Station 4 was located in the Wilmington River near the junction of Wilmington and Cabbage islands, where the clams occurred in approximately 0.2 m of water at mean low water.

The shell-length to dry-weight (DW) relationship was determined for *M. lateralis* (n = 100). After clams were measured to the nearest mm, the flesh was removed and dried to constant dry weight at 80°C for 48 h.

Secondary production was calculated using the instantaneous growth model of Waters and Crawford (1973):

$$P = G\bar{B}$$

where P = production in grams $\cdot$ m^{-2}, G = instantaneous

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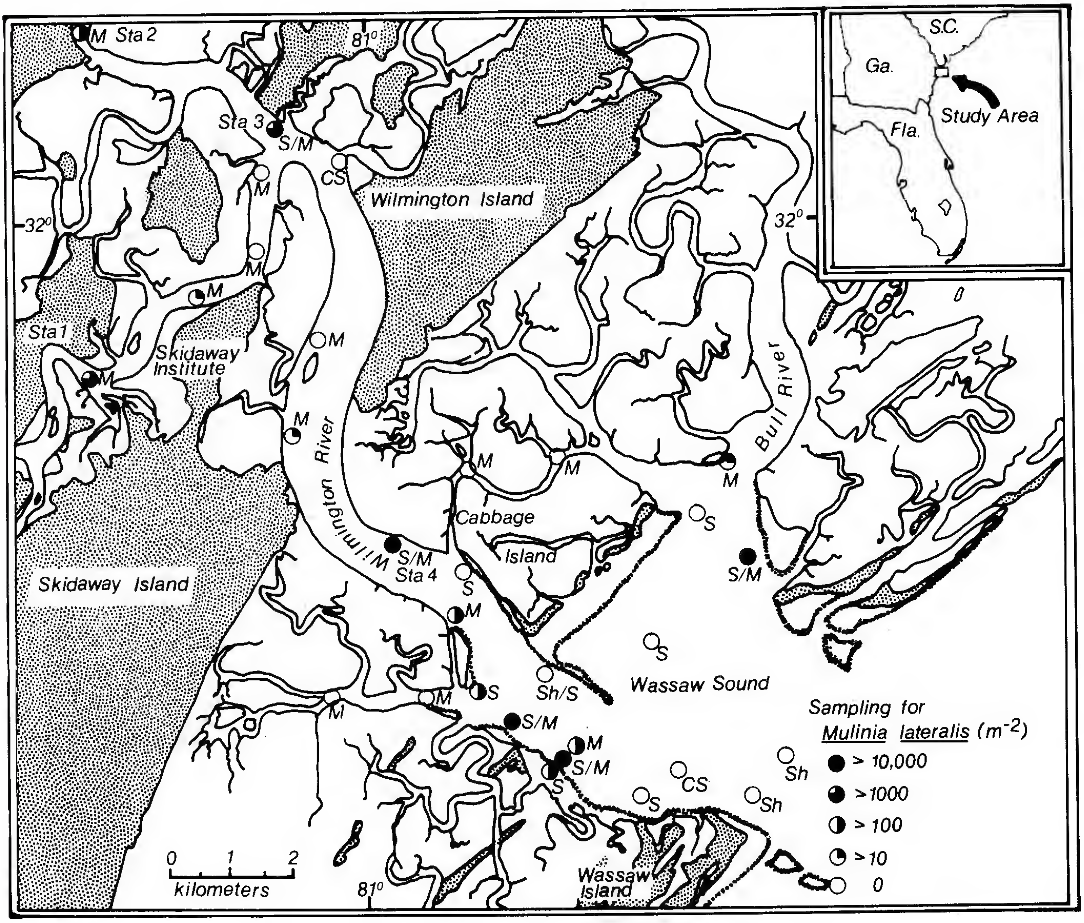

Figure 1. The distribution and relative abundance of *Mulinia lateralis* in Wassaw Sound, Georgia. Letters below the density symbols refer to substrate type: sh = shell, cs = coarse sand, s = sand, s/m = sandy mud, and m = mud.

growth for the time interval, and $\bar{B}$ = mean standing crop between given time intervals ($\bar{B} = [B_t + B_{t+1}]/2$). Instantaneous growth rate (G) is calculated as $\ln(W_t/W_o)$ where o and t represent the beginning and end of each time interval. Annual production is equal to the summation of the individual intervals' production estimates. Individual weights for the table were obtained by taking the mean of the clam lengths per month per station and applying that value to the shell-length to dry-weight regression equation.

Growth was determined by plotting the mean weight of the clams against time. Mean weights were determined using monthly mean shell lengths and converting to biomass.

RESULTS

Clams were absent or at low densities ($< 10 \cdot m^{-2}$) from 1977 to winter 1981. In January 1981 newly set clams were found throughout the Sound. Clams set intertidally to a depth of 7 m, with heaviest settings in the outer Sound (up to $63{,}000 \cdot m^{-2}$). Inshore of Skidaway and Wilmington islands, densities were $< 2000 \cdot m^{-2}$. Densities also varied with sediment type (Fig. 1). Clams had average densities of $10{,}161 \pm 19{,}475$ (SD) $\cdot m^{-2}$ in sandy mud, 277 ± 522 (SD) $\cdot m^{-2}$ in mud, 263 ± 468 (SD) $\cdot m^{-2}$ in sand, and were absent in coarse sand and shelly bottoms. In areas where the substrate changed from sand to mud, clams were more dense in the sand-to-mud interphase.

Densities increased at the four stations from January to February and then declined. Some specimens of *M. lateralis* in Wassaw Sound were mature and ripe in April but there was no new recruitment. None were found at Sta 1, 2, and 3 after April. Clams persisted at Sta 4 until August (Fig. 2). Densities varied greatly from a low of $525 \cdot m^{-2}$ at Sta 2 to

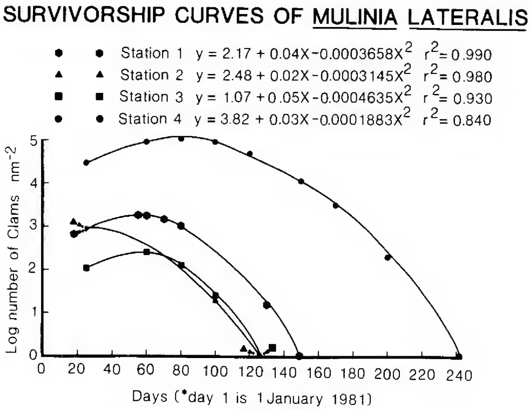

Figure 2. Survivorship curves for *Mulinia lateralis* at Stations 1 through 4. Day one is 1 January 1981.

a high of 63,168 • m^{-2} at Sta 4 in February. From January to March, individuals declined from 63,168 to 17,346 • m^{-2} at Sta 4; similar declines occurred at the other stations from February to April.

Histograms show changes in clam size with time and because there was only a single set, cohort production at the four stations could be estimated (Fig. 3).

The regression equation of shell length (SL) in cm to mean dry weight (DW) in grams is:

$$g\ DW = 0.01095\ (SL\ cm)^{2.968},\ r^2 = 0.94$$

and compares well to other bivalves (Winberg 1971). Changes in biomass with time were examined by the equation:

$$\bar{w} = at^b$$

where $\bar{w}$ = mean dry weight and t = time in days from settlement at each of the stations. The estimate of initial settlement was the beginning of January. By using monthly data points, the prediction was made by varying the day of settlement until the highest correlation coefficient was obtained. The best fit (r^2 = 0.99) was obtained when 1 or 2 January was used as the day of initial settlement.

Exponential growth rates were highest at Sta 3 and lowest at Sta 4 (Fig. 4). Slow individual growth rates at Sta 4 probably resulted from the high clam densities at that station.

Cohort production, standing crop, and cohort turnover ratios varied from a high production value of 325 g DW • m^{-2} • 7 mo^{-1} with a high standing crop of 513.44 g DW • m^{-2} at Sta 4 to a low production value of 0.29 g DW • m^{-2} • 4 mo^{-1} and low standing crop of 0.60 g DW • m^{-2} at Sta 2.

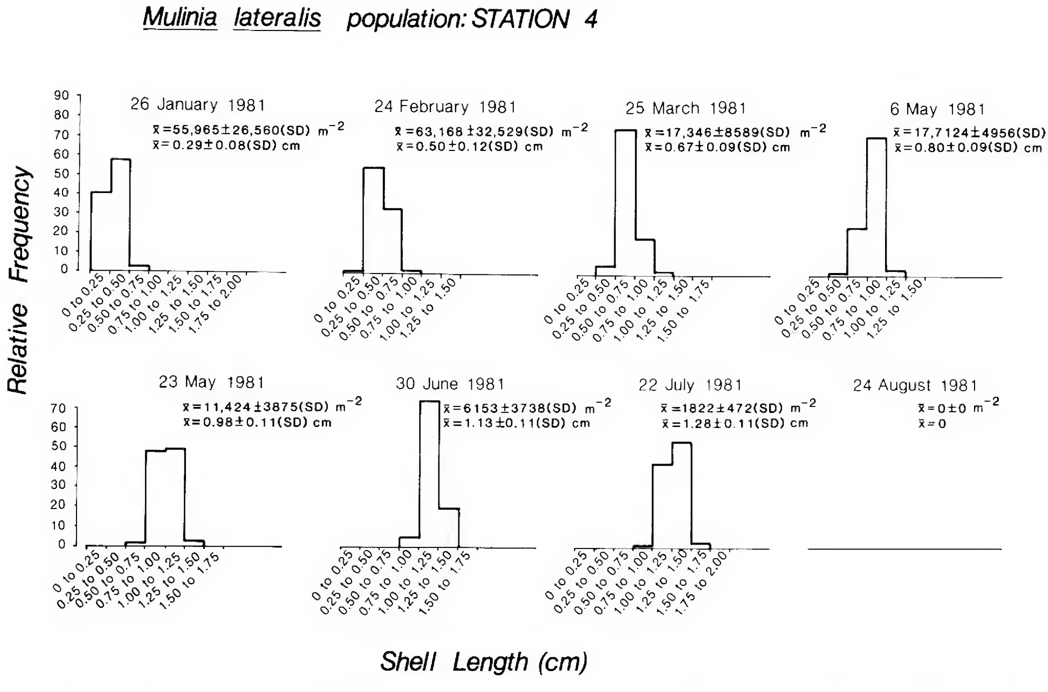

Figure 3. Monthly histograms for Station 4 showing changes in number • m^{-2}, average size, and the formation of only one cohort.

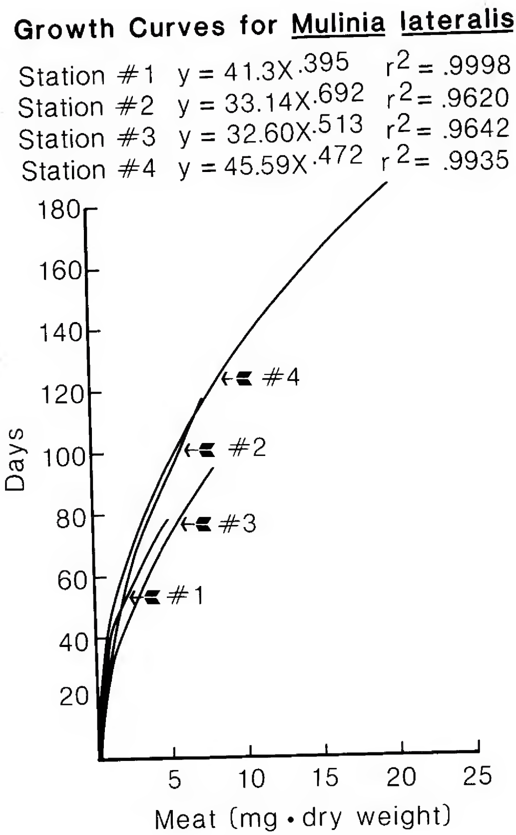

Figure 4. Growth rates for *Mulinia lateralis* at Stations 1 through 4.

Cohort production was estimated at 7.3 g DW • m^{-2} • 3 mo^{-1} with a standing crop of 9.19 g DW • m^{-2} and 4.12 g DW • m^{-2} • 4 mo^{-1} with a standing crop of 8.05 g DW • m^{-2} at Sta 1 and 3, respectively. Cohort turnover rates (P/B) ranged from a low of 1.93 for Sta 2 to a high of 4.40 for Sta 4 with Sta 1 and 3 having ratios of 2.38 and 2.05, respectively. The differences in estimates were attributed to differences in densities in clams. The higher the densities, the higher the production, standing crop, and turnover ratio (Table 1).

DISCUSSION

Salinity is a major regulator of benthic populations (Wells 1961) and year-to-year excessive salinity depression in winter/spring appears to regulate the annual recruitment of *M. lateralis* in Wassaw Sound. Low salinity (< 20 ppt) occurred during the winters from 1977 to 1980, during the period of normal reproduction which could affect gamete and larval development and survival. Larval development of *M. lateralis* is most successful (> 70%) from 22.5 to 30 ppt but can occur as low as 15 ppt (Calabrese 1969). Larval

TABLE 1

Cohort production by instantaneous growth method, cohort turnover ratio, mean density of clams for duration of population, and the duration of the population for Stations 1 through 4. Cohort production is in grams dry weight m^{-2} per duration of the population.

	Cohort* Production	Cohort* P/$\overline{B}$	Mean* Monthly Density (± SD)	Duration of Population
Station 1	7.29	2.38	1437±304	January to March
Station 2	0.29	1.93	148±252.6	January to April
Station 3	4.12	2.05	462±517	January to April
Station 4	325.28	4.44	24,770±24,540	January to July

* Based on less than one year, i.e., 3 mo for Sta 1, 4 mo for Sta 2 and 3, and 7 mo for Sta 4.

survival and growth is optimum at 20 to 27.5 ppt.

The distribution of animals within estuarine systems is generally related to salinity (Wells 1961, Menzel 1964, Wass 1965). Other environmental factors associated with salinity reductions, however, could be responsible for the lack of successful annual recruitment of *M. lateralis* in Georgia. For instance, with heavy freshwater runoff, a major shift in water mass could affect larval transport and settlement as well as changes in primary production. Furthermore, heavy runoff could increase the amount of suspended sediments as well as alter bottom sediments. Davis (1960) showed that growth and survival of clam (*Mercenaria mercenaria*) eggs and larvae was correlated to the type and concentration of various suspended material. Instability of the bottom surface can result in clogged filtering structures of suspension feeders, burying newly settled larvae or discouraging settling of suspension feeding bivalves (Rhoads and Young 1970).

Total cohort production was 100 times greater at Sta 4, located in the more saline region of the outer Sound, than at Sta 1 and 3 in the inner Sound. Further, Sta 1 and 3 were 24 and 14 times, respectively, more productive than Sta 2 located in the area of lowest salinity. This resulted from clam density and duration of the various populations. Clams at Sta 4 were dense and survived for 7 mo, while those at Sta 2 had a low density and survived 4 mo.

Populations of *M. lateralis* were quickly decimated following a heavy set in January 1981. Mortality probably resulted from predation by blue crabs *Callinectes sapidus* Rathbun. An abundance at all stations of shell fragments characteristic of crab predation (MacKenzie 1977) suggested heavy predation by the blue crab, a major predator of adults of *M. lateralis* (Virnstein 1977). Mortality of *M. lateralis* also resulted from the moon snail *Polinices duplicatus* (Say) as determined by type of bore hole (Carriker 1951), accounted for a small percentage of the monthly losses at Sta 4. Mean clam mortalities caused by snails were: 0, 504, 231, and 1008 clams • m^{-2} in February, March, April, and May,

TABLE 2

Annual production and P/B ratios of species of bivalves (production in g Ash Free Dry Weight m^{-2} unless otherwise stated). Bivalve age is in years.

Species	Production g AFDW m^{-2} yr^{-1}	P/$\bar{B}$ (yrs.)	Max. Age	Locality	Reference
Geukensia demissus* (Dillwyn)	3.34	?	0.28	Georgia, U.S.A.	Keunzler 1961
Tagelus divisus (Spengler)	21.0 g DW	1.78	2	Biscayne Bay, FL	Fraser 1967
Tellina martinicensis (Orbigny)	0.23 g DW	2.40	2	Biscayne Bay, FL	Penzias 1969
Chione cancellata (Linné)	8.90 g DW	0.42	7	Biscayne Bay, FL	Moore & Lopez 1969
Dosinia elegans (Conrad)	0.13 g DW	1.25	2	Biscayne Bay, FL	Moore & Lopez 1970
Anodontia alba (Link)	14.09 g DW	1.43	?	Biscayne Bay, FL	Moore & Lopez 1972
Mya arenaria (Linné)	11.60 g DW	2.54	3	Petpeswich Inlet, Can.	Burke & Mann 1974
Mya arenaria (Linné)	2.66	0.5	8	Lynher Estuary, U.K.	Warwick & Price 1975
Scrobicularia plana (da Costa)	0.48	0.20	9	Lynher Estuary, U.K.	Warwick & Price 1975
Macoma balthica (Linné)	0.31	0.90	6	Lynher Estuary, U.K.	Warwick & Price 1975
Macoma balthica (Linné)	1.93 g DW	1.53	3	Petpeswich Inlet, Can.	Burke & Mann 1974
Macoma balthica (Linné)	3.40	1.93	8.10	Grevelingen Estuary, Netherlands	Wolff & deWolf 1977
Macoma balthica (Linné)	0.94	1.00	8.10	Grevelingen Estuary, Netherlands	Wolff & deWolf 1977
Ensis siliqua (Linné)	1.37	0.27	10	Carmarthen Bay, South Wales	Warwick et al. 1978
Cerastoderma edule (Linné)	0.21	0.20	7	Lynher Estuary, U.K.	Warwick & Price 1975
Cerastoderma edule (Linné)	29.25	1.59	5	Southampton Waters, U.K.	Hibbert 1976
Cerastoderma edule (Linné)	71.36	1.10	5	Southampton Waters, U.K.	Hibbert 1976
Cerastoderma edule (Linné)	46.44	2.61	5	Southampton Waters, U.K.	Hibbert 1976
*Cerastoderma** edule* (Linné)	10.21	0.69	3.5	Grevelingen Estuary, Netherlands	Wolff & deWolf 1977
*Cerastoderma** edule* (Linné)	119.82	2.59	3.5	Grevelingen Estuary, Netherlands	Wolff & deWolf 1977
*Cerastoderma** edule* (Linné)	51.76	1.13	3.5	Grevelingen Estuary, Netherlands	Wolff & deWolf 1977
Venerupis aurea (Gmelin)	0.70	1.11	5	Southampton Waters, U.K.	Hibbert 1976
Venerupis aurea (Gmelin)	1.25	1.10	5	Southampton Waters, U.K.	Hibbert 1976
Venerupis decussata (Linné)	0.21	0.52	?	Southampton Waters, U.K.	Hibbert 1976
Venerupis decussata (Linné)	0.60	0.28	?	Southampton Waters, U.K.	Hibbert 1976
Donax vittatus (da Costa)	0.72	2.10	2.5	Carmarthen Bay, South Wales	Warwick et al. 1978
Venus striatula (da Costa)	0.62	0.41	10	Carmarthen Bay, South Wales	Warwick et al. 1978
Tellina fabula (Gmelin)	0.29	0.90	6	Carmarthen Bay, South Wales	Warwick et al. 1978
Tellina deltoides	2.35	1.42	4	Westernport Bay, Australia	Robertson 1979
Abra alba (Wood)	1.45	2.0	1.2	Concarneau Bay, France	Glemarec and Menesquen 1980
Crassostrea virginica (Gmelin)	4132 Kcal	2.01	2	South Carolina, U.S.A.	Dame 1976
Mytilus edulis (Linné)	3.68	1.00	?	Southampton Waters, U.K.	Hibbert 1976
Mytilus edulis (Linné)	4.82	1.00	?	Southampton Waters, U.K.	Hibbert 1976
Mytilus edulis (Linné)	29.43 KJ y^{-1}	?	7	Lynher Estuary, U.K.	Bayne & Worrall 1980
Mytilus edulis (Linné)	14.40 KJ y^{-1}	?	7	Cattewater Estuary, U.K.	Bayne & Worrall 1980
Mytilus edulis (Linné)	790.0	?	1	Nyckelbyviken Bay, Sweden	Loo & Rosenburg 1983
Mytilus edulis (Linné)	648.0	?	1	Nyckelbyviken Bay, Sweden	Loo & Rosenburg 1983
Mytilus edulis (Linné)	476.0	?	1	Nyckelbyviken Bay, Sweden	Loo & Rosenburg 1983
Mulinia lateralis (Say)	7.29 DW	2.38	0.25	Georgia, U.S.A.	This study
Mulinia lateralis (Say)	0.29 DW	1.93	0.33	Georgia, U.S.A.	This study
Mulinia lateralis (Say)	4.12 DW	2.05	0.33	Georgia, U.S.A.	This study
Mulinia lateralis (Say)	325.28 DW	4.44	0.58	Georgia, U.S.A.	This study
Mercenaria mercenaria (Linné)	62.82	3.02	1	Georgia, U.S.A.	Walker 1984
Mercenaria mercenaria (Linné)	23.71	1.85	1	Georgia, U.S.A.	Walker 1984
Mercenaria mercenaria (Linné)	133.60	3.38	1	Georgia, U.S.A.	Walker 1984
Mercenaria mercenaria (Linné)	0.51	0.25	9	Georgia, U.S.A.	Walker 1984
Mercenaria mercenaria (Linné)	6.15	0.18	34	Georgia, U.S.A.	Walker 1984
Mercenaria mercenaria (Linné)	18.53	0.17	30	Georgia, U.S.A.	Walker 1984
Mercenaria mercenaria (Linné)	0.24	0.25	9	Georgia, U.S.A.	Walker 1984
Mercenaria mercenaria (Linné)	6.57	0.19	34	Georgia, U.S.A.	Walker 1984
Mercenaria mercenaria (Linné)	6.49	0.22	30	Georgia, U.S.A.	Walker 1984
Mercenaria mercenaria (Linné)	3.99	0.52	8	Southampton Waters, U.K.	Hibbert 1976
Mercenaria mercenaria (Linné)	14.00	0.28	8	Southampton Waters, U.K.	Hibbert 1976
Mercenaria mercenaria (Linné)	6.19	0.17	9	Southampton Waters, U.K.	Hibbert 1976

* Given as *Modiolus demissus* in Keunzler (1961).

** Given as *Cardium edule* in Wolff and deWolf (1977).

TABLE 3

Some literature values for annual production (values in g Ash Free Dry Weight) of marine communities.

Locality	Production g AFDW · m^{-2} · yr^{-1}	Source
Long Island Sound, U.S.A.	8.0 to 64.5	Sanders 1956
Lynher Estuary, U.K.	13.3	Warwick & Price 1975
Southampton Waters, U.K.	220.0	Hibbert 1976
Grevelingen Estuary, Netherlands	0.1 to 219.9	Wolff & deWolf 1977
Carmarthen Bay, South Wales	25.8	Warwick et al. 1978

respectively. These values represented 0, 1.1, < 1, and 16% of total mortality. The spot *Leiostomus xanthurus* Lacepède is also a major predator of *M. lateralis* (Virnstein 1977); those caught in June had been feeding primarily on *M. lateralis* (personal observations).

Production estimates of *M. lateralis* ranged from 0.3 g DW · m^{-2} · 4 mo^{-1} to 325 g DW · m^{-2} · 7 mo^{-1} and are comparable to production data for other bivalves (Table 2) and benthic communities (Table 3). Cohort turnover ratios were considerably higher in Wassaw Sound, however, than those cited for other bivalves because the population studied was comprised only of young individuals. Turnover ratios decreased with increase in age of organisms (Nichols 1975, Warwick 1980, Walker 1984). The short-term production rate, i.e., the rate for the 3 to 7 mo that *M. lateralis* was present, was higher than reported for other bivalves. Thus, at least for a short period of time, *M. lateralis* effectively exploits available food resources and in turn can be a significant source of food for predators; however, year-to-year variations in production that resulted from recruitment failure that were caused by low winter salinities also caused a significant instability in the availability of this clam to predators.

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ULTRASTRUCTURE OF RODLET CELLS: RESPONSE TO CADMIUM DAMAGE IN THE KIDNEY OF THE SPOT *LEIOSTOMUS XANTHURUS* LACÉPÈDE

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ABSTRACT Rodlet cell ultrastructure was studied in normal and cadmium-damaged kidney tissues of the spot *Leiostomus xanthurus,* an estuarine teleost. Rodlet cells in control fish occurred in all parts of the nephron except the renal corpuscle, were oblong to pear-shaped (about 5x10 μm), and contained up to 30 rodlet bodies, a basally situated nucleus, poorly developed mitochondria, and a filamentous cortex. Desmosomes and tight junctions joined rodlet cells to kidney epithelial cells. After cadmium exposure, rodlet cells showed a range of responses from secretory stimulation to necrosis. Rodlet bodies, which were membrane-bound, club-shaped granules, were secreted by a merocrine process, apparently aided by contraction of the filamentous cortex. New rodlet bodies were assembled in the Golgi apparatus. Mitochondria hypertrophied and developed well-defined cristae. The ultrastructural organization of the rodlet cells in this study and their responses to stimuli suggest that these are tissue or host cells rather than parasites as proposed by some authors. Further studies, however, are needed to confirm the nature of these cells.

INTRODUCTION

Rodlet cells occur frequently in fish tissues and have long been the subject of controversy over whether they are protozoan parasites (Thélohan 1892) or tissue cells (Plehn 1906). Most ultrastructural studies agree that the principal cytologic features of these cells are rodlet bodies, a filamentous cortex that lies beneath the plasma membrane, and a basally situated nucleus. However, there is little agreement on the nature of the rodlet cell and reports on ultrastructural details vary. Some consider the cells to be parasites because of their widespread distribution in tissues or because of the resemblance of some rodlet cell organelles to those of apicomplexan protozoans (Bannister 1966, Iwai 1968, Mourier 1970, Flood et al. 1975, Mayberry et al. 1979). Others consider rodlet cells to be unicellular glands in which the rodlet bodies are secretory granules formed in the Golgi apparatus from material synthesized in the rough endoplasmic reticulum (RER) (Leino 1974, Desser and Lester 1975, Morrison and Odense 1978, Mattey et al. 1979).

In most studies, rodlet cells have been examined in normal tissues. Few studies have involved rodlet cells in pathological or toxicological situations. In a study on the effect of cadmium on the kidney of the spot *Leiostomus xanthurus,* an estuarine teleost (Hawkins et al. 1980), we found that parts of the renal tubule had abundant rodlet cells. Since cadmium caused severe damage to renal tubular epithelial cells, we thought it worthwhile to examine the ultrastructural changes in rodlet cells in cadmium-damaged renal tubules.

MATERIALS AND METHODS

Twenty-six spot, 10–15 cm in total length, were collected by trawl, seine, and hook and line from the Mississippi Sound. Specimens were taken to the laboratory and either processed immediately or maintained in glass aquaria containing filtered and circulating artificial sea water with a salinity of 15–25 ppt. Fish were killed by pithing. Kidneys were fixed *in situ* in either 3.0% glutaraldehyde in 0.1 M phosphate buffer or in Karnovsky's fixative (Karnovsky 1965) in 0.1 M cacodylate buffer. For transmission electron microscopy (TEM), tissues were minced, rinsed in the appropriate buffer and postfixed in 1.0% osmium tetroxide. Some tissues were *en bloc* stained with aqueous uranyl acetate. Tissues were dehydrated in ethanol and embedded in epoxy resin. Thin sections were stained with lead citrate and examined with a Phillips 301 or Siemens Elmiskop 1A electron microscope. For orientation, semithin sections (1–2 μm thickness) were cut, mounted on glass slides, and stained with toluidine blue.

For scanning electron microscopy (SEM), whole kidneys were dissected as described above and allowed to fix for 2 h to several days and then cut with a razor blade into sections about 2 mm thick. The sections were postfixed for 1 h in buffered 1.0% osmium tetroxide, dehydrated in ethanol and critical point dried using CO_2. Tissues were sputter-coated with gold and examined with an ETEC Autoscan.

Procedures for exposing fish to cadmium have been described (Hawkins et al. 1980). Briefly, spot were exposed in static aquaria to levels of cadmium chloride from 1 to 100 ppm for 48 h. Tissues were processed for electron microscopy as described above.

RESULTS

Rodlet cells in control kidney

Rodlet cells occurred in the epithelium of the neck segment, proximal tubule, collecting tubule, and ureteric duct. In control kidneys, rodlet cells were not found in renal corpuscles, blood vessels, or hemopoietic tissues. SEM of

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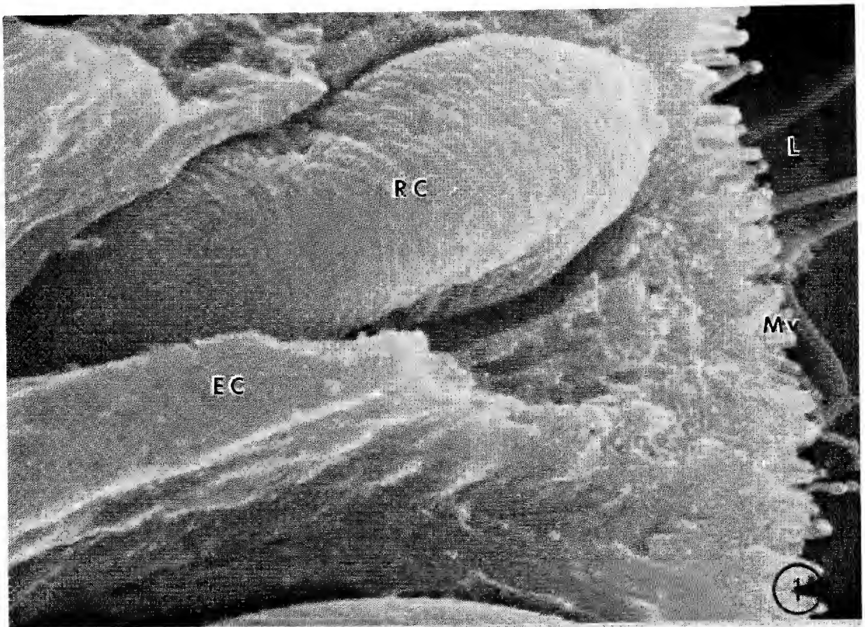


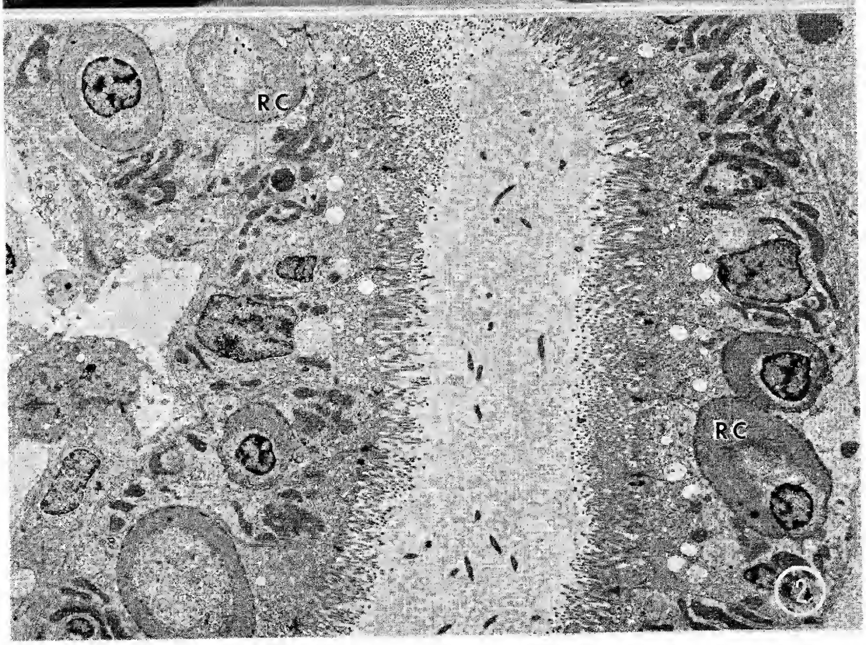


Figure 1. Scanning electron micrograph of a rodlet cell (RC) between epithelial cells (EC) of the ureteric duct. Note ridges and furrows on surface of rodlet cell. Duct lumen (L); microvilli (Mv). X 13,200

Figure 2. Transmission electron micrograph of rodlet cells (RC) in proximal tubule. X 3,200

ureteric duct epithelium showed that the rodlet cells were oblong to pear-shaped and wedged between the epithelial cells (Figure 1). The rodlet cell surface formed circumferential ridges and furrows. The apex of the rodlet cell often bordered on the lumen and occasionally issued microvillus-like processes into the duct lumen. The space that separated the rodlet cell from surrounding epithelial cells was not present in TEM samples or in SEM samples that were prepared by freeze-cracking (unpublished observations). In some proximal tubules, rodlet cells (about 5X10 μm) were almost as abundant as tubule epithelial cells (Figure 2).

The structure and organization of most rodlet cell organelles conformed with those of other species. Some important features are described for comparison with cadmium-exposed cells but are not illustrated.

The rodlet cell apex faced the tubule lumen. The basally situated nucleus (3–4 μm in diameter) contained dense, marginated chromatin. As many as 30 club-shaped membrane-bound rodlet bodies, each with an electron-dense core, extended from near the nucleus to the cell apex. Golgi complexes were rarely seen. Elongate, sinuous, poorly differentiated mitochondria (about 0.15 to 0.30 μm in diameter) occurred near the apex. A filamentous cortex (about 0.5 μm thick) which lay beneath the plasmalemma, except at the apex, contained thick filaments (20 nm in diameter) oriented around the long axis of the cell and thin filaments (6–8 nm in diameter) that were not regularly oriented. Microtubules (about 10 nm in diameter) ran along the inner aspect of the cortex from the apical to the basal region. Dense plaques situated 15–20 nm from the plasmalemma lined the cell at regular intervals. Rodlet cells and tubular epithelial cells were connected by desmosomes and tight junctions.

Some rodlet cells appeared open to the tubule lumen (Figure 3). Membrane-bound rodlet bodies were seen in the tubule lumen near such cells. The nuclei of these rodlet cells resembled those of normal resting cells. Usually, the tubule lumens that contained rodlet cell debris were compressed and also contained debris from the tubular epithelium.

Cadmium-exposed kidney

Exposure to cadmium levels greater than 10 ppm for 48 h damaged proximal tubular epithelium (Hawkins et al. 1980). Concurrently, changes took place in rodlet cells. Rodlet cells were not disrupted or damaged as severely as the tubular epithelial cells. Detached rodlet cells, however, lay among epithelial cells, in tubule lumens, and in Bowman's space of the renal corpuscle (Figure 4). Some rodlet cells were joined by desmosomes (Figure 5). In many cells, the filamentous cortex was thickened and the dense plaques were nearly continuous. Vesicles often occurred within the filamentous cortex or between it and the plasmalemma. Some rodlet cells appeared to expel their rodlet bodies by a merocrine process whereby the membrane surrounding a rodlet body became continuous with the plasmalemma (Figure 6). Other organelles of these secreting cells were similar to those of resting cells.

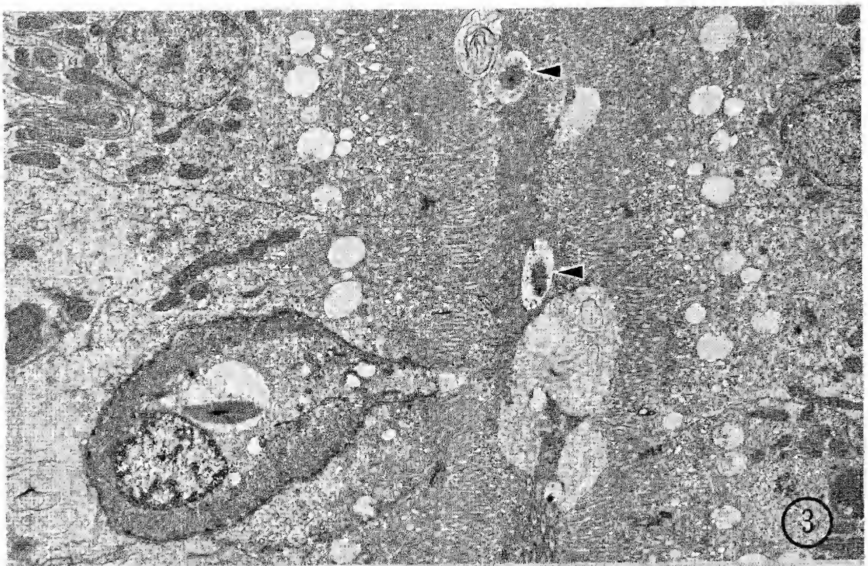
Rodlet cells appeared to reform rodlet bodies in the Golgi apparatus (Figure 7). The dense core of forming rodlet bodies was smaller than in mature rodlet bodies. The origin of the dense core was not determined. RER was abundant in the supranuclear cytoplasm, especially near developing rodlet bodies. The mitochondria of these cells were rounder, larger, and cristae better developed than in control rodlet cells (Figure 8). Nucleoli, usually absent in control rodlet cells, were sometimes present in these cells.

In some rodlet cells, the area between the filamentous cortex and the cytoplasm was not distinct and the cortex lacked subplasmalemmal dense plaques. These cells often contained dense spherical structures 0.5 to 1.0 μm in diameter (Figures 4, 9, 10). Rodlet bodies were similar to those in control rodlet cells. Mitochondria were often swollen and vacuolated. Membrane-bound inclusions of homogenous material, membranes, and vesicles frequently occurred in these cells. Centrioles were often present in the apical cytoplasm (Figure 10). Nuclei contained one or more dense spherical inclusions that were as large as 2.0 μm in diameter. Otherwise, the nucleus was electron lucent with a flocculent nucleoplasm (Figure 9).

Many rodlet cells appeared to be in late stages of necrosis. The plasmalemma was often disrupted, especially at the apex. Nuclei were pyknotic and sometimes in the process of being expelled (Figure 11). The fibrillar cortex was intact although dense plaques were lacking. Also lacking were the microtubules that ran in the junction between the cytoplasmic core and the fibrillar cortex. Mitochondria were round with prominent cristae and a few dense deposits. Occasionally, degenerating rodlet cells were phagocytosed by monocytic macrophages (Figure 12).

DISCUSSION

The origin and functions of rodlet cell mitochondria and rodlet bodies are disputed by the tissue-cell (Leino 1974, Desser and Lester 1975, Morrison and Odense 1978, Mattey et al. 1979) and parasite (Bannister 1966, Mourier 1970, Mayberry et al. 1979) proponents. Distinct, ovoid mitochondria with prominent cristae occur in immature, developing rodlet cells (Leino 1974, Desser and Lester 1975) whereas mitochondria in mature rodlet cells are tubular with indistinct cristae (Bannister 1966, Wilson and Westerman 1967, Mourier 1970, Leino 1974, Desser and Lester 1975, Morrison and Odense 1978, Barber et al. 1979). Mayberry et al. (1979) described structures reported to be mitochondria in mature rodlet cells as micronemes. Micronemes are osmiophilic, cord-like organelles of apicomplexan parasites (Chobotar and Scholtyseck 1982). Rodlet cells in control spot kidney had tubular mitochondria with indistinct cristae similar to the mitochondria in mature rodlet cells of other species. After exposure to nephrotoxic



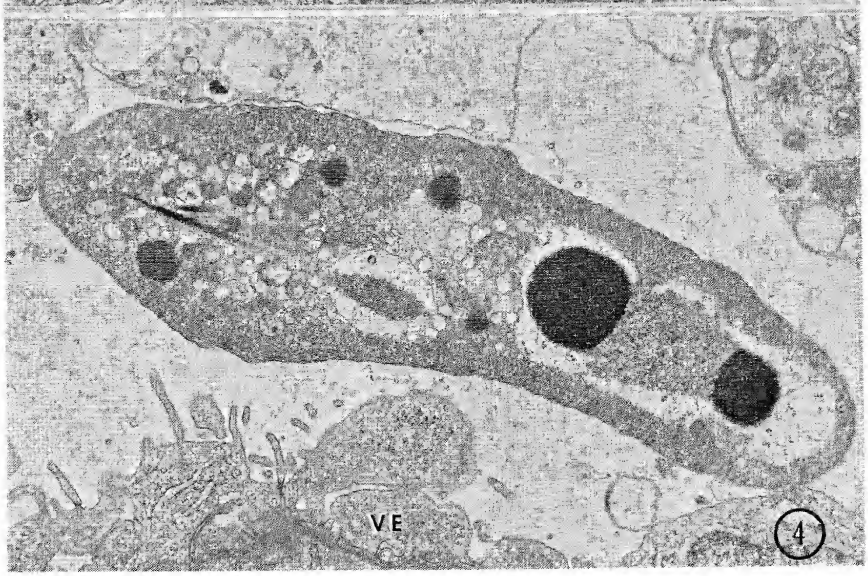


Figure 3. Membrane-bound rodlet bodies (arrowheads) in lumen of proximal tubule. Note apex of rodlet cell appears to open into lumen. Also note other debris in lumen. X 4,100

Figure 4. Detached rodlet cell in Bowman's space following cadmium exposure. Note dense nuclear and cytoplasmic bodies in rodlet cell. Visceral glomerular epithelium (VE). X 6,400

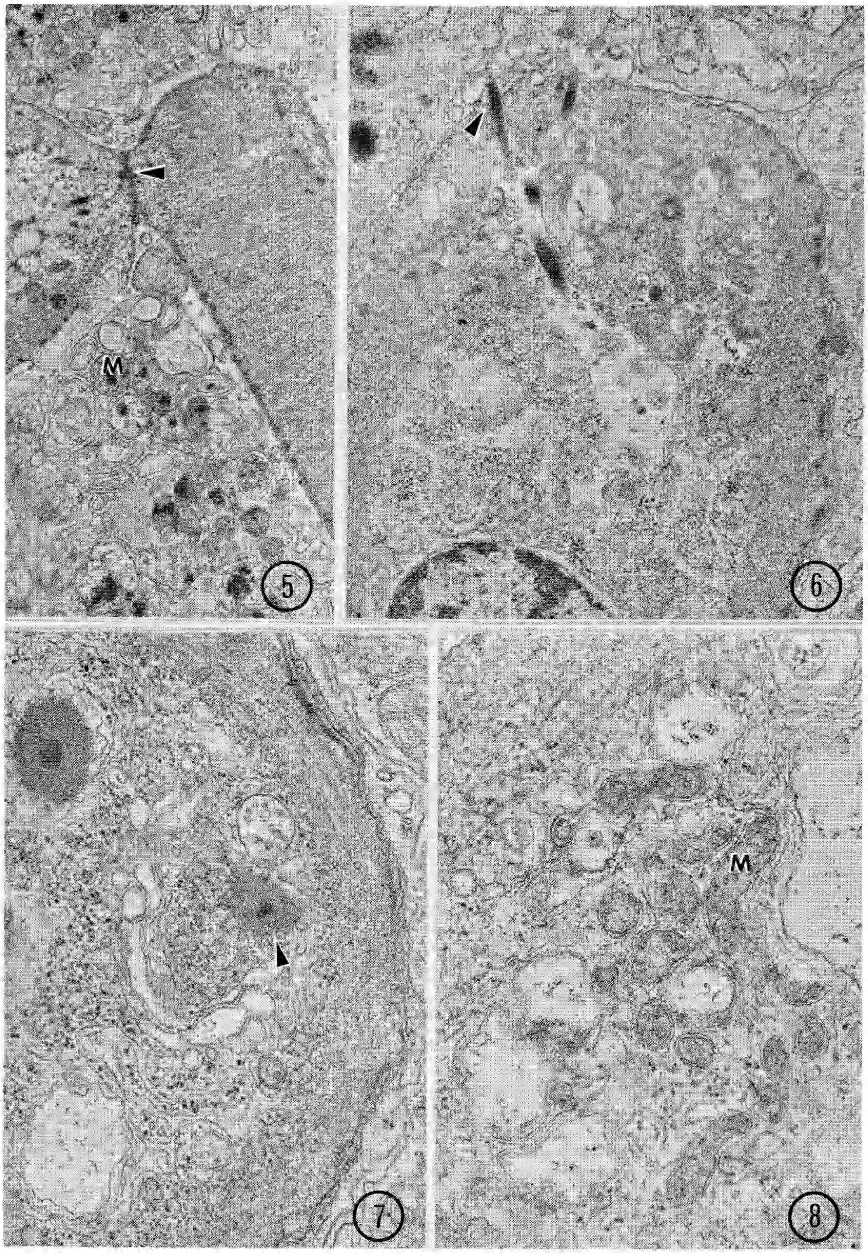


Figure 5. Desmosome (arrowhead) between two rodlet cells. Note disrupted and damaged mitochondria (M) of renal tubule epithelium. Cadmium-exposed. X 8,400

Figure 6. Rodlet body apparently being secreted without disruption of plasma membrane. Note that at the arrowhead, the plasma membrane becomes continuous with membranes of the rodlet body vacuole. Cadmium-exposed. X 17,300

Figure 7. Immature rodlet body (arrowhead) associated with Golgi-like membranes and vesicles. Cadmium-exposed. X 27,600

Figure 8. Rodlet cell mitochondria (M) following cadmium damage. X 30,800

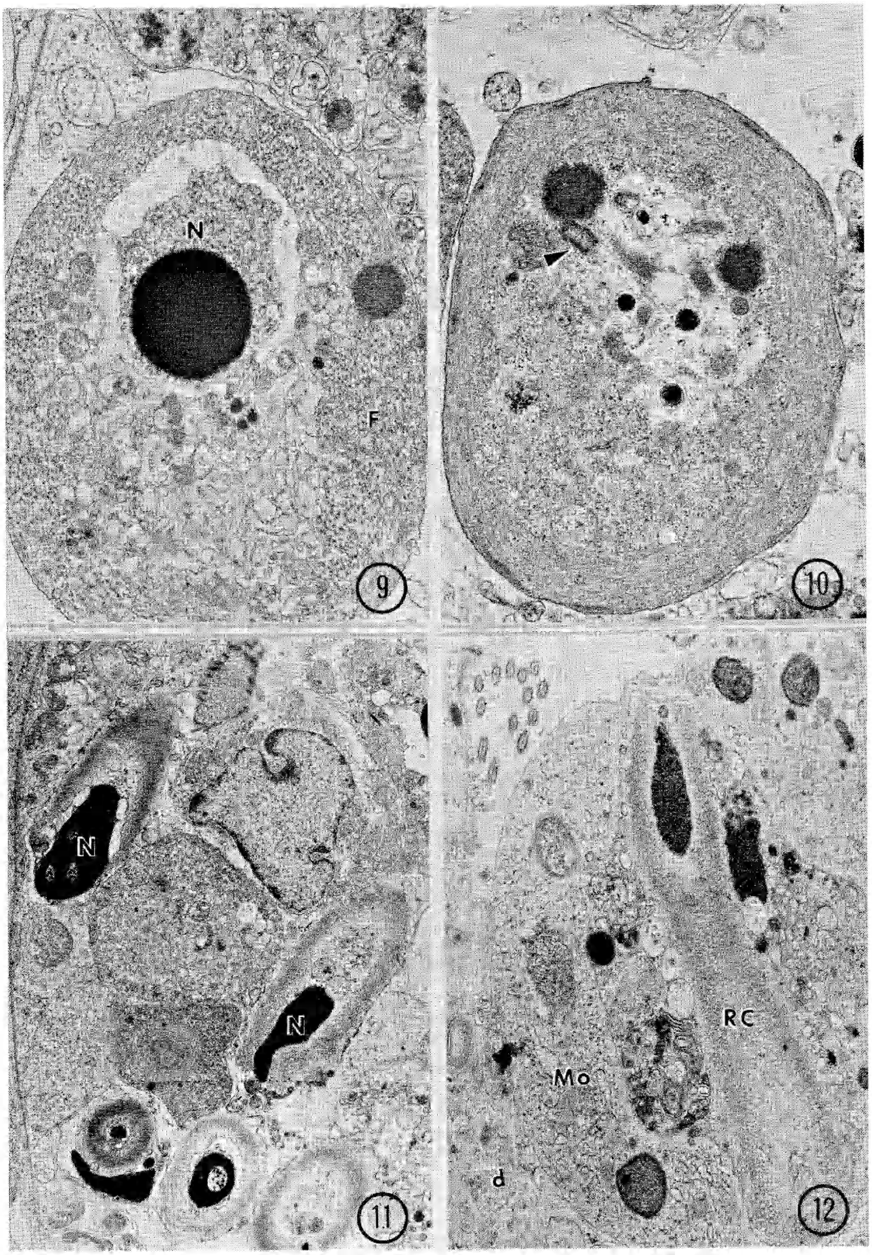


Figure 9. Rodlet cell following cadmium damage showing swollen filamentous cortex (F) and dense bodies in nucleus (N) and cytoplasm. X 12,800

Figure 10. Centriole (arrowhead) in rodlet cell following cadmium exposure. X 15,000

Figure 11. Necrotic rodlet cells following cadmium exposure. Note pyknotic nuclei (N). X 4,000

Figure 12. Rodlet cell (RC) phagocytosed by monocyte (Mo) following cadmium exposure. X 6,600

cadmium levels, however, the tubular mitochondria became ovoid with prominent cristae. Thus, these structures were clearly identifiable as mitochondria.

Cytochemical studies of nucleic acids in rodlet bodies disagree. Leino (1982) identified carbohydrates and protein in the granular matrix of the rodlet body and determined that the rodlet core contained protein but no carbohydrate or nucleic acids. Based on RNAase digestion studies, Barber et al. (1979) suggested that rodlet body cores contained RNA. Bielek and Viehberger (1983), supporting the parasitic nature of rodlet cells, identified DNA in rodlet cores by fluorescence staining and DNAase digestion studies.

Several studies showed that rodlet bodies are synthesized in Golgi apparatus of immature cells (Leino 1974, Desser and Lester 1975, Barber et al. 1979, Mattey et al. 1979). In spot exposed to cadmium, rodlet cells apparently were stimulated to secrete their rodlet bodies which were replaced by the Golgi apparatus. The release of rodlet bodies occurred by a merocrine process without disruption of the plasmalemma and was accompanied by contraction of the filamentous cortex. Leino (1974) suggested that rodlet cell secretion was holocrine and that the secretion involved contraction of the filamentous cortex, disruption of the apical plasmalemma, and expulsion of the rodlet cell contents. Mayberry et al. (1979) who referred to rodlet bodies as rhoptries, coccidian organelles that appear to aid in the penetration of the host cell by the coccidium (Chobotar and Scholtyseck 1982), observed rodlet cell organelles and whole rodlet cells in the lumens of epithelial tissues and suggested that this resulted from handling or processing damage whereas intact rodlet cells were parasites that had left the host tissues. Mattey et al. (1979) also maintained that the appearance of holocrine secretion by rodlet cells was the result of handling or fixation damage. In the spot, holocrine secretion by rodlet cells also appears to be artifactual because tubule lumens that contained rodlet cell debris often contained epithelial cell debris as well. However, it is possible, as Leino (1974) suggested, that sloughing of most or all of the rodlet cell contents is the final stage of the cycle of this cell. If the normal secretion of the rodlet cell is merocrine, then the function of the filamentous cortex is not clear. Perhaps contraction of the filamentous cortex is necessary to aid in expelling the large rodlet body with its apparently rigid core.

Rodlet cell junctional complexes vary among species. Desmosomes occur between rodlet cells and epithelial cells in several species of freshwater fishes (Leino 1974, Mattey et al. 1979) and tight junctions between rodlet cells and epithelial cells in the operculum and gill raker of the white sucker *Catostomus commersoni* Lacépède (Desser and Lester 1975). Mourier (1970), who considered rodlet cells to be parasites, reported desmosomes between rodlet cells but not between rodlet cells and tubule epithelial cells in the kidney of the stickleback *Gasterosteus aculeatus* L. Rodlet cells in cadmium-damaged spot kidney were occasionally joined by desmosomes although such junctions in normal kidney were not observed. The significance of this is not clear. Intercellular junctions were not reported between immature or developing rodlet cells or between such cells and epithelial cells by Leino (1974) or Desser and Lester (1975). The ability of rodlet cells to form desmosomes and tight junctions is not shared with any apicomplexan parasite.

The present study confirms neither the parasitic nor the tissue-cell nature of the rodlet cell. Confirmation must await studies characterizing rodlet cell DNA and immunological properties and comparing these with known fish cells. It is likely that preparations rich in rodlet cells such as the spot proximal tubule could be exploited for these studies. Nevertheless, the ultrastructural organization of rodlet cells in control and cadmium-damaged renal tubules of the spot suggests to us that these are tissue cells rather than apicomplexan parasites.

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The Epiphytic Diatom Flora of Two Sargassum Species

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SHORT COMMUNICATIONS

THE EPIPHYTIC DIATOM FLORA OF TWO *SARGASSUM* SPECIES

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ABSTRACT The epiphytic diatom flora on the brown algae *Sargassum natans* (L.) J. Meyer and *S. fluitans* Børgesen were investigated and compared. A total of 50 taxa representing 21 genera were identified. The most abundant taxa were *Amphora exigua* Greg., *A. coffeiformis* (Ag.) Kütz., *Synedra fasciculata* (Ag.) Kütz., *Cocconeis pseudodiruptoides* Foged, and *Navicula ramosissima* (Ag.) Cleve. Comparisons of the dominant species and diversity statistics characterizing the two samples indicated the two brown algal species supported nearly identical epiphytic diatom floras.

INTRODUCTION

Most of the recent studies of Gulf Coast benthic diatoms have involved sediment-associated floras and pertinent examples include Wood (1963), Sullivan (1978), Cook and Whipple (1982), and Stowe (1982). Although epiphytic diatoms on seagrasses in the Gulf of Mexico have been studied (Montgomery 1978, Sullivan 1979), there has been only one investigation of diatoms epiphytic on attached seaweeds from the Gulf Coast (Medlin 1983). The studies of Grunow (1867) (Honduras), Hentschel (1921) (Sargasso Sea), and Carpenter (1970) (western Sargasso Sea) are the only reports of diatoms epiphytic on *Sargassum* species. The purpose of this report is to describe and compare the epiphytic diatom floras on *Sargassum natans* (L.) J. Meyer and *S. fluitans* Børgesen.

Sargassum natans and *S. fluitans* are the two most common species of *Sargassum* found in the Gulf of Mexico, and both species range throughout the Gulf, in particular coastal areas where drifting plants wash ashore. Unlike most species of *Sargassum*, *S. fluitans* and *S. natans* are obligate drifters with *S. natans* often comprising 95% of the mass of floating communities (Conger et al. 1972).

MATERIALS AND METHODS

Samples of *S. natans* and *S. fluitans* were collected with a hand net from a single station in the Gulf of Mexico (longitude 29°31′N and latitude 93°31′W) approximately 22 km southwest of Calcasieu Pass, Louisiana, on 25 June 1982. Composite samples of each host (including 2 cm of stipe, 4–5 pneumatocysts, and 2 or 3 blades) were boiled in HNO_3 with $K_2Cr_2O_7$ to oxidize all organic matter. A portion of each sample was mounted in Hyrax for identification and counting with an Olympus BHTU microscope. A sample from each host plant consisted of exactly 500 valves from five counts of 100 valves where each count was made from a separate slide prepared from the composite sample. After each sample had been analyzed taxonomically, the two floras were compared using Stander's (1970) Similarity Index (SIMI) and the Shannon-Weiner Information Index (Pielou 1975).

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RESULTS AND DISCUSSION

A total of 50 taxa representing 21 genera were identified in the two samples. Forty-three taxa were collected from *S. fluitans* and 39 from *S. natans.* The identity and relative abundance of each diatom taxon is listed in Table 1. The dominant genera, in terms of taxa encountered, were *Mastogloia* (8), *Navicula* (7), *Amphora* (4), and *Nitzschia* (4). The five most abundant taxa of the pooled sample, in order of decreasing abundance, were as follows: *Amphora exigua, A. coffeiformis, Synedra fasciculata, Cocconeis pseudodiruptoides,* and *Navicula ramosissima.* The first four taxa were also the four most abundant diatoms on both *S. natans* and *S. fluitans.* These five accounted for 65% of the 1,000 valves counted. Additional scans of the slides revealed several taxa not included in the counts. These taxa were: *Achnanthes hauckinana* Grun., *Cymbella pusilla* Grun., *Eunotogramma laeve* Grun., *Navicula comoides* (Ag.) Perag., *Nitzschia frustulum* (Kütz.) Grun., *N. microcephala* Grun., and *N. palea* (Kütz.) Grun.

Of the 50 taxa identified, 6 taxa are new records for the north-central Gulf: *Amphora bigibba, Cocconeis pseudodiruptoides, Licmophora remulus, Mastogloia ovalis, M. pusilla* var. *subcapitata,* and *Synedra provincialis* var. *tortuosa.* All of the taxa except *C. pseudodiruptoides* and *M. pusilla* var. *subcapitata* have been previously reported from the greater Gulf of Mexico (Conger et al. 1972; Sullivan 1981, Maples 1983a and 1983b). *Cocconeis pseudodiruptoides* was described by Foged (1975) as a littoral species along the Tanzania Coast. The chief difference between this species and *C. diruptoides* Hust. is the presence of a dilated central area which reaches the margin of both

TABLE 1

Relative abundance (expressed as number of valves in a sample of 500) of epiphytic diatom taxa on *Sargassum fluitans* and *S. natans* from the coastal marine waters of southwestern Louisiana. Collected on 25 June 1982. ΣN = both samples pooled as one.

Diatom taxon	*Sargassum* *fluitans*	*Sargassum* *natans*	ΣN
Achnanthes biasolettiana (Kütz.) Grun.	15	10	25
A. brevipes var. *intermedia* (Kütz.) Cl.	1	–	1
Amphora angusta var. *ventricosa* Greg.	4	6	10
A. bigibba Grun.	4	–	4
A. coffeiformis (Ag.) Kütz.	114	84	198
A. exigua Greg.	103	98	210
Bacillaria paxillifer (Müll.) Hendey	4	1	5
Cocconeis pseudodiruptoides Foged	36	60	96
C. scutellum Ehr.	8	10	18
Coscinodiscus radiatus Ehr.	1	1	2
Cyclotella atomus Hust.	20	4	24
C. striata (Kütz.) Grun.	4	6	10
C. meneghiniana Kütz.	1	–	1
Diploneis weissflogi (A.S.) Cl.	2	–	2
Fragilaria construens var. *venter* (Ehr.) Grun.	2	1	3
Grammatophora oceanica Ehr.	1	1	2
Licomphora abbreviata Ag.	8	16	24
L. cf. *debilis* (Kütz.) Grun.	4	4	8
L. remulus Grun.	2	2	4
Mastogloia acutiuscula Grun.	1	2	3
M. binotata (Grun.) Cl.	4	3	7
M. crucicula (Grun.) Cl.	8	6	14
M. erythraea Grun.	–	10	10
M. exigua Lewis	–	18	18
M. ovalis A.S.	2	–	2
M. pusilla Grun.	4	32	36
M. pusilla var. *subcapitata* Hust.	6	4	10
Navicula ramosissima (Ag.) Cl.	36	14	50
N. amphipleuroides Hust.	4	–	4
N. abunda Hust.	8	8	16
N. incomposita var. *minor* Hagelstein	–	3	3
N. tripunctata var. *schizonemoides* (V.H.) Patr.	1	2	3
Navicula sp. #1	2	2	4
Navicula sp. #2	1	2	3
Nitzchia bicapitata Cleve	1	1	2
N. dissipata (Kütz.) Grun.	4	–	4
N. fasciculata (Grun.) Grun.	–	2	2
N. gandersheimiensis Krasske	6	1	7
Pleurosigma normanii Ralf.	4	–	4
P. salinarum (Grun.) Grun.	1	–	1
Psammodiscus nitidus (Greg.) Round & Mann	3	–	3
Rhopalodia gibberula (Ehr.) Müll.	4	2	6
R. operculata var. *producta* Grun.	–	1	1
Synedra fasciculata (Ag.) Kütz.	48	58	106
S. provincialis var. *tortuosa* Grun.	4	6	10
Striatella unipunctata (Lyngb.) Ag.	10	10	20
Thalassionema nitzschioides (Grun.) V.H.	–	1	1
Thalassiosira eccentrica (Ehr.) Cl.	1	–	1
T. leptopus (Grun.) Hasle & Fryxell	–	1	1
Trachysphenia acuminata Perag.	2	1	3
H′	2.796	2.755	——
S	43	39	50

the raphe and rapheless valves in the former. It is interesting to note that the illustrations of *C. dirupta* Greg. reported on *Sargassum* by Carpenter (1970) are identical to *C. pseudodiruptoides.* Apparently this record of *C. pseudodiruptoides* is new for the United States, which is interesting since it constituted nearly 10% of the epiphytic diatom flora in the pooled *Sargassum* samples.

A comparison of the epiphytic diatom flora on the two *Sargassum* species revealed few differences. The species diversities (H′ $\log_2$) for each of the *Sargassum* samples were almost identical (Table 1). A comparison of the structural similarity (SIMI) of the two samples revealed a value of 0.931. SIMI has the limits of 0 and 1; the larger the SIMI value, the greater the similarity between two samples. A total of 32 taxa were recorded as common to both *Sargassum* species (Table 1). Of the 18 taxa found only on one of the *Sargassum* species, all but 2 of these taxa (*Mastogloia erythraea* and *M. exigua*) were represented by 4 valves or less. This data, along with very similar values of H′ and S for the two samples (Table 1) and a high SIMI value, indicates the two brown algal species supported nearly identical epiphytic diatom floras.

A comparison was made of the results from this study with others on the epiphytic diatom flora of *Sargassum.* Grunow (1867) recorded 91 species from the coastal waters of Honduras and only 7 of these were encountered in the present study. None of the species found to be common to both studies was abundant in the present study. Since Hentschel (1921) recorded only one taxon (*Cocconeis* sp.), no meaningful comparison can be made. Carpenter (1970) identified only 10 taxa to species from samples collected in the western Sargasso Sea, only 5 are common to the present study. Although Carpenter (1970) collected the same species of *Sargassum* as examined in the present study, the dominant taxa were quite different. *Mastogloia binotata* was the dominant taxon in 6 of his 7 samples, but constituted less than 1 percent of the total valves in the pooled samples of the present study. It is interesting to compare the low number of epiphytic diatom taxa (10) reported by Carpenter (1970) on open-ocean *Sargassum* as opposed to the much higher numbers found on coastal *Sargassum*, 91 by Grunow (1867) and 50 in the present study. The differences between these studies may be related to unknown physiochemical differences among the habitats and the small number of samples investigated.

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Sexual Dimorphism in Species of Raninoides (Brachyura: Raninidae) and the Status of *Raninidoides schmitti* Sawaya, 1944

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SEXUAL DIMORPHISM IN SPECIES OF *RANINOIDES* (BRACHYURA: RANINIDAE) AND THE STATUS OF *RANINOIDES SCHMITTI* SAWAYA, 1944

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ABSTRACT The frog crab *Raninoides schmitti* was described from São Paulo, Brazil, as closely related to *R. loevis.* Detailed comparison shows *R. schmitti* to be a junior synonym of *R. loevis.* Absence of information detailing sexual dimorphism of species in the genus *Raninoides* contributed to the designation of a dimorphic male as a discrete taxon. Examples of sexual dimorphism within the genus *Raninoides* are described.

INTRODUCTION

Thirty-five extant species of frog crabs are currently assigned to the family Raninidae which is composed of ten Recent genera. This group appears to be most numerous in the western Pacific where approximately 22 species have been recorded. Nine species in four genera are represented in the western Atlantic. Members of the genus *Raninoides* H. Milne-Edwards, 1837, are the subject of this report.

Reports of sexual dimorphism within frog crabs have been largely confined to that exhibited in the type species, *Ranina ranina* (Linnaeus, 1758). It is well documented (Barnard 1950, Fielding and Haley 1976) that the dimorphism affects the anterolateral spines of the carapace in that taxon. However, until this report other species were not known to show strong sexual dimorphism. Within the genus *Raninoides,* sexual dimorphism is exhibited by the form of the cheliped and in some species the anterior spines of the carapace and the male gonopod.

Material examined –Raninoides benedicti: 1 ♂, 47.5 mm, 27 Aug. 1976, Isla Chepillo, Bay of Panama, coll. Gordon Hendler. *Raninoides loevis:* (Florida Department of Natural Resources, Marine Research Laboratory), FSBC I 2649, 9 Mar. 1966, 2 males (35.2–38.1); FSBC I 2648, 3 Mar. 1966, 1 male (39.2); FSBC I 2737, 11 Apr. 1966, 1 male (37.2); FSBC I 19940, 18 June 1966, 1 male (42.3); FSBC I 19963, 25 Oct. 1967, 1 male (42.2); EJ 66-444, 20 Nov. 1966, 1 male (39.1); FSBC I 19955, 14 Mar. 1967, 1 male (36.8); FSBC I 19967, 14 Nov. 1967, 1 male (36.7); EJ 67-113, 12 Apr. 1967, 1 male (39.8); FSBC I 19936, 19 Jan. 1966, 1 male (38.7); FSBC I 19961, 7 Aug. 1967, 4 males (38.0–41.6); FSBC I 19945, 6 Nov. 1966, 1 male (36.7); FSBC I 19948, 6 Jan. 1967, 1 male (42.0). *Raninoides louisianenis:* USL 836 (University of Southwestern Louisiana), 30 Oct. 1975, 1 male (61.2); TAMU 2-0961 (Texas A&M University), 19 Nov. 1968, 1 male (27.2); TAMU 2-1264, 28 Jan. 1971, 2 males (52.6–53.6); TAMU 2-1272, 23 June 1972, 2 males (59.1–61.2); TAMU 2-1269, 5 Feb. 1972, 1 male (49.5); USA 100401 (University of South Alabama), 28 Aug. 1976, 3 males (49.8–52.3); GCRL 1125 (Gulf Coast Research Laboratory), 2 Apr. 1980, 1 male (57.3). *Raninoides schmitti:* Museu Nacional do Brasil, Nov. 1955, 1 male (45.0).

Remarks – Adult dimorphic males of *R. louisianensis* Rathbun, 1937, *R. loevis* (Latreille, 1825), and the Pacific species *R. benedicti* were examined. In *R. louisianensis,* adult males with a carapace length of over 50 mm often exhibit dimorphism in the shape of the above mentioned features. The chelae and frontal spines are perhaps the most evident of the dimorphic characters (Figure 1A and 1B).The movable finger of the claw in females and young males is very nearly equal in length to the fixed finger. In dimorphic males, however, the movable finger greatly exceeds the length of the fixed finger, sometimes by up to twice the length. The terminal portion of the finger becomes strongly curved, and the small spine at the base of the finger decreases in size. The propodus also increases in size, although the ventral spines of the palm do not. This gives the impression of a decrease in size of the spines of the palm. The second obvious dimorphic character in some species is the development of a sharply curved hepatic spine on the carapace. This feature is not as obvious at the early stages as is the increased finger length; however, a formidably curved spine is the eventual result. A third dimorphic character evident in the males of *R. louisianensis* is the development of the three spines which surround the apex of the first male gonopod. Among larger dimorphic males, these accessory spines become elongated and slightly curved.

Raninoides loevis and *R. benedicti* exhibit dimorphism in the shape of the chela only. No males examined showed evidence of dimorphism in the shape of the frontal spines of the carapace or the apical spines of the gonopods. The single dimorphic male of *R. benedicti* examined closely parallels the situation found in *R. loevis,* its Atlantic cognate. *Raninoides benedicti* closely agrees in the shape of the first gonopod with published accounts (Knight 1968) and no evidence of curvature was found in the frontal spines of the carapace.

Rathbun (1937) recognized seven nominal species of the frog crab genus *Raninoides* H. Milne-Edwards, 1837, from

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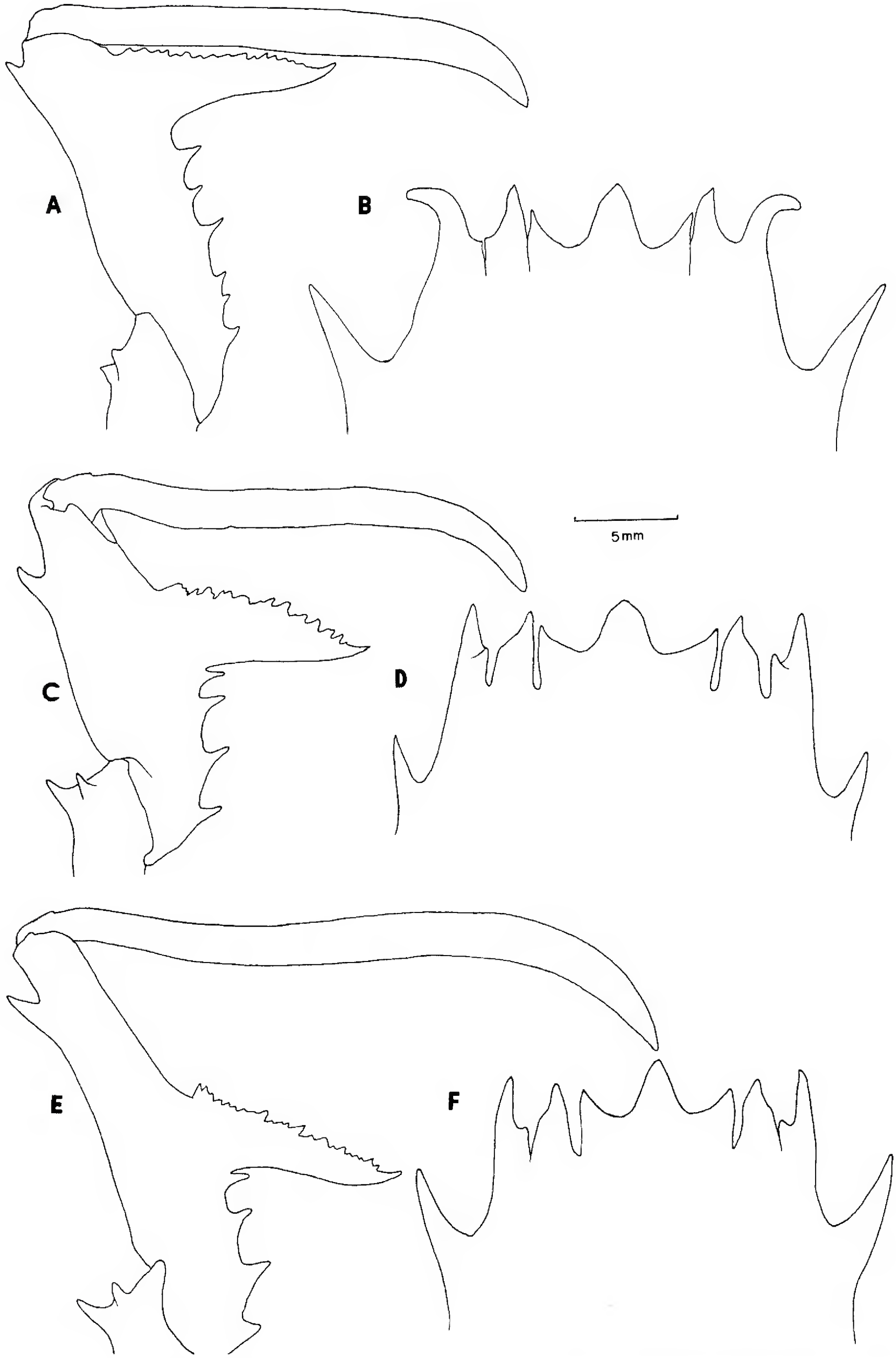

Figure 1. (A) Cheliped and (B) frontal carapace region of *R. louisianensis;* (C) cheliped and (D) frontal carapace region of *R. loevis*; (E) cheliped and (F) frontal carapace region of *R. benedicti.*

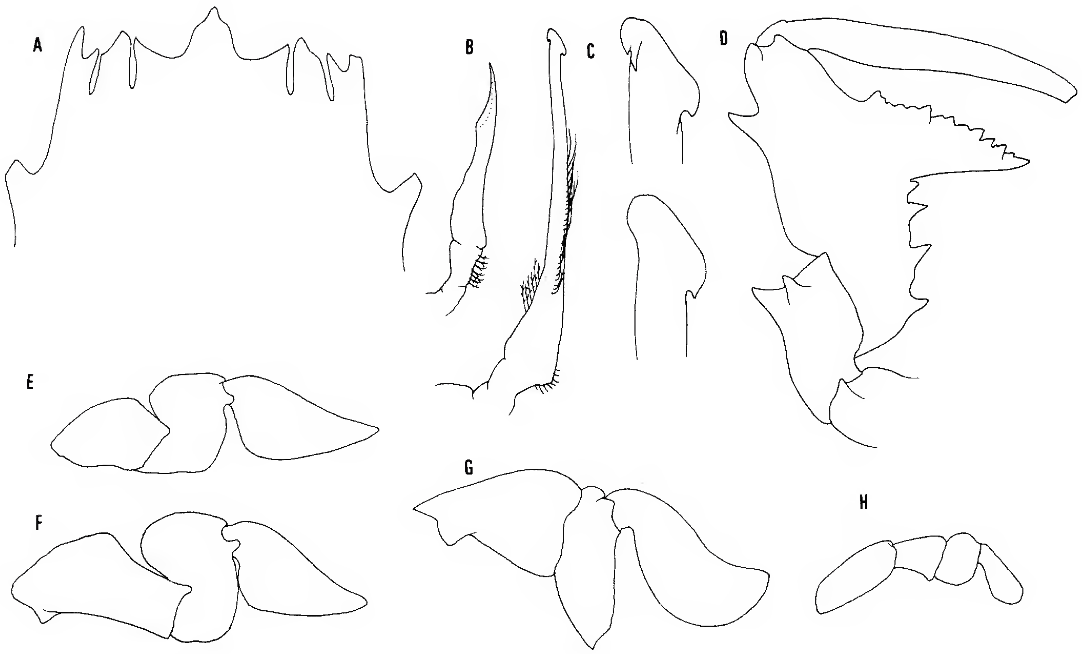

Figure 2. ***Raninoides schmitti*** **(topotype). (A) Frontal carapace region, (B) pleopod 2, (C) pleopod 1 (detail), (D) cheliped, (E) ultimate segments of pereopods 2, (F) 3, (G) 4, and (H) 5.**

American waters. A single species, *R. schmitti* Sawaya, 1944, has been described off Brazil since Rathbun's report. Three species assigned to this genus were recently removed or designated synonyms. *Raninoides fossor* H. Milne-Edwards and Bouvier, 1923, is considered by Manning (1975) to be a junior synonym of *Notosceles chimmonis* Bourne, 1922, and not a member of the western Atlantic fauna. *Raninoides nitidus* A. Milne-Edwards, 1880, was shown to be a senior synonym for *Lyreidus bairdii* Smith, 1881, and was removed to *Lyreidus* de Haan, 1841, by Goeke (1980). Characters of diagnostic value used to separate the closely related genera *Notosceles* Bourne, 1922, and *Raninoides* are listed by Goeke (1981) and the eastern Pacific species *Raninoides ecuadorensis* Rathbun, 1935, was transferred to *Notosceles.*

Raninoides schmitti Sawaya, 1944, was described from a single male from the beach of São Sebastio, São Paulo, Brazil. Sawaya (1944:141) states "*R. schmitti* is distinct from *R. loevis* principally by the size of the dactylus in relation to the immobile finger of the cheliped and the not curved lateral spines." Additional specific characters for *R. schmitti* are listed as the two spine-like processes of the sternum between the bases of pereopods 1 and 2, and the "process" opposite the distal spine of the merus of the cheliped. A pronounced asymmetry in the size of the chelipeds is evident from the figures of the holotype and Sawaya noted this as either a specific character or attributed this to regeneration. The size of the unique holotype was also given as 49 mm, "the biggest hitherto noted in the genus." The only additional record for *R. schmitti* is based on a large male (carapace length of 45 mm) from São Paulo by Gomes Corrêa (1970). That specimen (Figure 2) was collected by Sawaya in November, 1955, from Praia do Segredo, São Sebastiao, São Paulo, and was examined by me.

As was detailed previously, sexual dimorphism in the genus *Raninoides* affects the length of the dactylus of the chelipeds. In the taxa examined by this author, the dactylus of pereopod 1 is disproportionately lengthened and in some instances, the dactyl approaches twice the length of the fixed finger. This increase in length of the finger is not a specific character as it has been noted in congeneric species. Other features of the dactylus and propodus are affected as well. The small size of the right chela of the holotype is probably due to regeneration as all known raninids are homoisochelic.

The second character detailed by Sawaya (1944) is the pair of spine-like processes between the bases of pereopods 1 and 2. This feature has been noted by previous workers on other species of *Raninoides* and has been used as evidence for the separation of *Raninoides* from *Notosceles* (Bourne 1922; Serène and Umali 1972; Goeke 1981). This feature is evident in seven species of *Raninoides* that have been examined by me and is of generic value and

not a species specific character.

The "not curved lateral spines" listed by Sawaya (1944) is not a specific feature of value in separating *R. schmitti* from *R. loevis.* Considerable variation in the form of the lateral spines of *R. loevis* has been observed in material from the eastern Gulf of Mexico (Goeke, unpublished data). Gomes Corrêa (1970) illustrated distinctly curved lateral spines in the specimen identified by Sawaya as *R. schmitti* from the type-locality. These spines are now broken and I am not able to observe the degree of curvature.

A "process" of unspecified form is mentioned by Sawaya as opposite the distal spine of the merus of pereopod 1. No process other than a slight swelling at the carpal-meral articulation is indicated or could be located on the specimen examined by this author. This swelling is a normal condition within the group.

A final important consideration is the form of the gonopod of the male. This important taxonomic character is unique for each of the described species within *Raninoides* with the exception of *R. schmitti.* This feature was not discussed by Sawaya. The illustration of Gomes Corrêa (1970, Figure 35) closely resembles the previously published illustrations of *R. loevis* by Guinot-Dumortier (1960) and Knight (1968). The gonopod of the specimen examined (Figure 2C) agrees very well with those of *R. loevis* from the eastern Gulf of Mexico. Because of the examination of other specimens with small regenerative claws (*R. benedicti* from Panama) and the description of the form of sexual dimorphism found in crabs of the genus *Raninoides,* I consider *Raninoides schmitti* Sawaya, 1944, to be a junior synonym of *Raninoides loevis* (Latreille, 1825).

Four species of *Raninoides* are recognized by the author from American waters; 3 western Atlantic and 1 eastern Pacific. Eight species are now assigned to this genus, with the possibility that an additional species, *Raninoides barnardi* Sakai, 1974, will be transferred to *Notosceles.*

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A Record of *Bermudrilus peniatus* (Oligochaeta: Tubificidae) from the Gulf of Mexico

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A RECORD OF *BERMUDRILUS PENIATUS* (OLIGOCHAETA: TUBIFICIDAE) FROM THE GULF OF MEXICO

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ABSTRACT The marine tubificid *Bermudrilus peniatus* Erséus, 1979 (subfamily Phallodrilinae) is reported from off the west coast of central Florida, at about 75 m depth. The species was previously known only from coral reefs at Bermuda.

Bermudrilus peniatus is known only from medium to coarse sand in a depth of 10 to 15 meters in coral reefs at Bermuda (Erséus 1979). Recently when examining a collection of offshore oligochaetes from the eastern part of the Gulf of Mexico, I found a single specimen that extends considerably the known distribution of the species. Consequently, it is reported here.

The specimen originated from a Bureau of Land Management baseline study by personnel at Dauphin Island Sea Lab, Alabama. It was mounted whole in Canada balsam before examination and is deposited in the National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C.

Bermudrilus peniatus Erséus, 1979

Bermudrilus peniatus Erséus, 1979, pp. 425–426, fig. 4.

Type material – USNM 56314–56316, five specimens, all from the type locality.

Type locality – Southeast of Charles' Island, Bermuda, 15 m, medium to coarse sand.

Additional specimens in original material (author's collection) – Eight specimens; seven from the type locality and one from east side of Castle Roads, Bermuda, 10 m, coarse sand with gravel and pebbles.

New material examined – USNM 97379, one specimen from about 155 km west of Sarasota, west coast of Florida, USA, about 75 m, sediment unknown (collected 23 August 1977).

Remarks – The individual is 4.1 mm long and has 39 segments. It fits the original description except for some minor differences. There are 6 penial setae, 16–22 μm long, per bundle located ventrally in segment XI (Fig. 1). The funnel-shaped, cuticularized penes (Fig. 1) are 24–30 μm long with a base 10–11 μm wide and a midsection about 5 μm wide. As in the original material, the prostate glands are large and located anteriorly, with no posterior prostate glands present.

ACKNOWLEDGMENTS

I am indebted to Dr. M. Susan Ivester, for placing the material at my disposal.

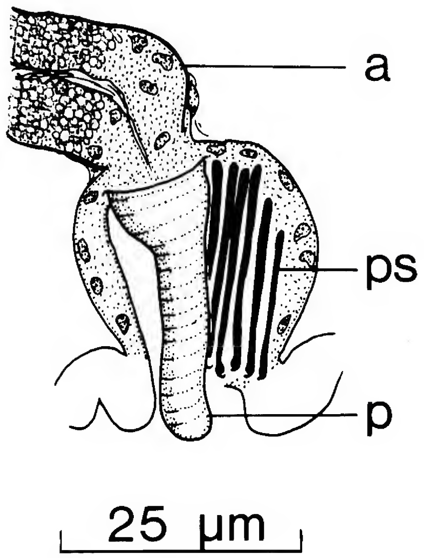

Figure 1. ***Bermudrilus peniatus*** **Erséus from off west coast of Florida showing ectal part of atrium (a), penis (p) and penial setae (ps).**

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Comments on Density Inversions in Marine Shallow Waters and Beyond

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COMMENTS ON DENSITY INVERSIONS IN MARINE SHALLOW WATERS AND BEYOND

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It has been shown within the past 70 years that salinity and thus density inversions are often detectible in shallow bays and estuaries. This terminology means that surface salinities are sometimes higher than those at lower depths. The first such discoveries in this country were made by Sumner, Louderback, Schmitt and Johnston (1914) in San Francisco Bay. They used Negretti-Zambra reversing thermometers for temperature and silver nitrate titration for salinity determination. These were by then considered to be classical methods and had been worked out in northern Europe, mostly in Scandinavia. They were introduced to the United States Gulf Coast and the authors in 1931 by Frank W. Weymouth, of Stanford University, who headed the Shrimp Investigations of the U.S. Bureau of Fisheries from 1930, which were later taken over by Milton J. Lindner.

Forrest V. Durand, as a cooperative agent of the Louisiana Department of Conservation, carried on the hydrographic work in Louisiana, mostly in Barataria Bay and adjacent offshore waters. The first author, as biologist for the Bureau, was a close observer, but of not much hydrographic assistance. Durand was under J. Nelson Gowanloch. After Durand left Louisiana the data were unfortunately misplaced.

Thirty-one years after Sumner et al. (1914), Gunter (1945) reported 5.5 percent inversions in 109 readings taken during a biological study of Copano and Aransas bays in Texas in the years 1941 and 1942.

Albert Collier, first marine biologist of the Texas Game, Fish, and Oyster Commission, had conducted a hydrographic survey in the same area in 1936 and 1937. During these years he took 385 salinity readings in Copano Bay and 874 in Aransas Bay at 47 station locations. He found 20.9 percent salinity inversions, 101 in Copano Bay and 144 in Aransas Bay, the higher salinity bay next to the sea.

There were 197 top and bottom equalities of salinity in Copano Bay and 85 in Aransas Bay. Copano is about 7 feet deep as compared to 11 feet for Aransas, the outer bay. In Copano Bay there were 14 readings of only 0.1 per mil difference in inversions, that is with the surface 0.1 parts per thousand higher in salinity. In Aransas Bay there were 17 such readings.

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The data used here were taken from Tables 5 and 6, pages 186–192 (Collier and Hedgpeth 1950). Collier's data had been transported around to various places between 1936 and 1949 and moved hurriedly three times in front of hurricanes. Finally they aroused the interest of Joel W. Hedgpeth who resurrected them and completed the writing of the Collier, Hedgpeth paper with the addition of the Laguna Madre data which Hedgpeth had collated and in part gathered himself. In the meantime various parts of Collier's data were lost or displaced but we have held to Tables 5 and 6 as stated above. These comprised 1,169 salinity readings.

Strangely enough, Collier and Hedgpeth did not mention salinity inversions, which they so carefully recorded in their data, nor did they refer to similar data collected by Sumner et al. (1914) or the previously published reference of Gunter (1945) in their own region. However, their work has been referred to as the seminal paper in shallow-water hydrography on the United States Gulf coast and the authors had many subjects to address.

In Copano Bay the inversions ranged from 0.1 parts to 2.9 parts per thousand difference. There were only two of the larger size with many more at lower ranges. In Aransas Bay there were much wider variations, 2 up to 12 per mil, which could be doubted except for other high readings at nearby stations. These high readings at the surface in Aransas Bay may have been due to overriding of Gulf water or current aberrations in turbulent waters. In any case it is not thought to be worthwhile to try to analyze these data further in view of the impossibility of determining what caused the high figure inversions.

In Aransas Bay there were 399 more salinity samplings than in Copano Bay. In Copano Bay 101 density inversions were found among 385 readings. In Aransas Bay there were 144 inversions at 785 stations. Thus in the lower bay there was a decrease in density inversions per number of stations. This is apparently a real difference with a confidence limit of $p = 0.95$. Aransas Bay is about 4 feet deeper than Copano and this may be an important fact but we cannot be sure that wind velocity and some other factor made a difference nearer the sea. In any case, if this inversion trend were to continue on into saltier water of the open sea, density inversions at the surface would decrease in number. These matters need to be studied with sensitive instruments near the surface of the ocean. However, we cannot expect that any effect of physical factors will change merely because

they are farther offshore. Thus it is to be assumed that winds and atmospheric conditions will affect the waters of the open sea in the same manner as they do in the bays. Thus it is expected that density inversions in surface waters will be found offshore, although the depth to which they extend is unknown. This should be a field for inquiry in the future because the situation remains very much as it was when Sverdrup stated, "..., but nothing is known as to the annual variation of salinity at subsurface depths, ..." (Sverdrup, Johnson and Fleming 1946, p. 146). In the past when salinity and temperature data were collected only at finite depths, oceanographers increased vertical spacing by wide intervals at sea when depth permitted, with some skipping of intervening phenomena.

Jacobs (1942) has given information on the evaporation rates in the Gulf of Mexico, the presumed basic cause of density inversions. In the open ocean, turbulence would not play such a strong part as we have implied above in the bays, channels, and confined waters.

Density inversions have been noted many times in Mississippi waters but the tables showing inversions are rather scarce and the matter is nowhere clearly discussed.

Charles Eleuterius (1973) in a processed report says of salinity on page 106, "During periods of high evaporation, the measurements in the surface layer of water were higher than those immediately beneath; however, the temperature differential substantiated the stability of this structure."

This is not the clearest possible language but it does mention the essential conditions for density inversions. They occur first at the surface due to evaporation, then sink to their own level of specific gravity, where essentially they disappear. The lighter, displaced water then rises to the surface where it is subjected to evaporation. Thus the process is cyclical and continuous at all water surfaces, varying with temperatures of the water and air, the water salinity, the percentage of water vapor in the air and the wind speed. It causes an exchange of various surface layers of water and deeper layers, varying with the numerous conditions listed above. It has not been studied thoroughly and carefully anywhere.

In the above discussion we have spoken of salinity inversions although the temperature readings at the same stations have substantiated the reality of density inversions based on both factors, salinity and temperature.

It seems to be of some importance to consider that the sinking of high-salinity water to its equilibrium level, and a compensating rise of water from a greater depth, is somewhat analogous to a breathing process at the surface of the sea modified by various climatic and atmospheric conditions, and results in modified exchange of water and atmospheric components. This process is continually carried on or "powered" so to speak by evaporation at the sea surface.

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A Preliminary Checklist of Epiphytic and Benthic Marine Diatoms of Louisiana

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A PRELIMINARY CHECKLIST OF EPIPHYTIC AND BENTHIC MARINE DIATOMS OF LOUISIANA

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ABSTRACT A checklist of diatoms collected from the various habitats in coastal salt marshes, estuaries, and nearshore Gulf waters of Louisiana has been compiled for the first time. The checklist includes 193 taxa (species and their varieties) in 38 genera. The largest number of taxa are species of *Navicula* and *Nitzschia* with 46 and 36, respectively. Future studies of the varied habitats along the Louisiana coast should result in many new additions to this preliminary checklist.

INTRODUCTION

The algal flora of coastal Louisiana has been variously studied since the first reports of Featherman (1871, 1872). Kapraun (1974) surveyed the marine benthic green, red, and brown algae found on jetty structures bordering Louisiana's marine passes. *Vaucheria* species were recorded by Pecora (1977, 1980) from coastal salt marsh habitats. Maples (1982) described an edaphic bluegreen algal community associated with a coastal salt panne in southwestern Louisiana. Checklists of marine planktonic diatoms in the nearshore waters of Louisiana are found in papers by Featherman (1871, 1872), Simmons and Thomas (1962), Bamforth (1974), Housley (1976), Fucik and El-Sayed (1979), and Maples (1983a). Studies of marine benthic diatoms have been largely centered in the Mississippi delta region of Louisiana. Cook and Whipple (1982) described the spatial and temporal distribution of edaphic diatom communities along a complex gradient from brackish to saline marshland. Stowe (1982) investigated the distribution of epiphytic diatoms on the culms of *Spartina alterniflora* Loisel. Maples (1983b) reported on the taxonomy, diversity, and similarity of benthic diatom assemblages on the pneumatophores of the black mangrove *Avicennia germinans* (L.) L., in a Louisiana salt marsh.

Kalinsky (1983) compiled a checklist of non-marine algae from Louisiana. Many species found in Louisiana by this author were not included in Kalinsky's (1983) checklist. An up-to-date list of diatoms in Louisiana's coastal environments was thought to be needed. In light of the reports of Wood (1963) and Medlin (1983) for Texas, and Sullivan (1981) for Mississippi, the present checklist contributes to our knowledge of the geographic distribution of marine diatoms.

Three different papers were used in the preparation of this checklist (Cook and Whipple 1982, Stowe 1982, Maples 1983b) as well as unpublished observations by this author. The present checklist is biased toward the epiphytic diatom flora of coastal salt marshes, but edaphic (sediment-associated) diatom taxa are included. A number of taxa are primarily freshwater forms, but these may be occasionally observed in brackish water habitats. The flora reported herein is of an edaphic or epiphytic nature, and represents marsh, estuarine, and nearshore habitats.

CHECKLIST FORMAT

For the purpose of this checklist, diatoms were considered to constitute the single class Bacillariophyceae. Genera are arranged alphabetically, and species with their varieties are arranged alphabetically within each genus following the format of Hendey's (1974) checklist for British marine diatoms. Species and their varieties collected only from the pelagic alga *Sargassum* are marked with an asterisk.

BACILLARIOPHYCEAE

ACHNANTHES Bory, 1822
- *biasolettiana* (Ag.) Grun.
- *brevipes* var. *intermedia* (Kütz.) Cl.
- *curvirostrum* Brun.
- *exigua* Grun.
- *hauckiana* Grun.
- *lanceolata* var. *dubia* Grun.
- *lemmermanni* Hust.
- *submarina* Hust.
- *subsessilis* Kütz.
- *temperei* M. Perag.

AMPHIPRORA Ehrenburg, 1843
- *alata* Kütz.
- *paludosa* W. Sm.

AMPHORA Ehrenburg, 1831
- *angusta* Greg.
  - var. *angusta*
  - var. *oblongella* Grun.
- *bigibba* Grun.
- *caroliniana* Giffen
- *coeffeiformis* (Ag.) Kütz.
- *exigua* Greg.

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granulata Greg.
laevis var. *perminuta* Grun.
libyca Ehr.
pediculus (Kütz.) Grun.
proteus Greg.
sabyii Salah
tenerrima Hust.
tenuissima Hust.
ventricosa Greg.
ANOMOENEIS Pfitzer, 1871
sphaeophora (Kütz.) Pfitzer
BACILLARIA Gmelin, 1778
paxillifer (Müll.) Hendey
BERKELEYA Greville, 1827
rutilans (Trent.) Grun.
CALONEIS Cleve, 1894
westii (W. Sms.) Hendey
CAMPYLOSIRA Grunow, 1882
alexandrica Salah
CAPARTOGRAMMA Kufferath, 1956
crucicula (Grun.) Ross
COCCONEIS Ehrenburg, 1838
fluviatilis Wallace
placentula Ehr.
var. *placentula*
var. *euglypta* (Ehr.) Grun.
pseudodiruptoides Foged*
scutellum Ehr.
var. *scutellum*
var. *parva* Grun.
CYCLOTELLA Kützing, 1833
atomus Hust.
caspia Grun.
comta (Ehr.) Kütz.
meneghiniana Kütz.
striata (Kütz.) Grun.
stylorum Brightwell
CYLINDROTHECA Rabenhorst, 1859
gracilis (Bréb.) Grun.
CYMATOSIRA Grunow, 1862
belgica Grun.
CYMBELLA Agardh, 1830
pusilla Grun.
DENTICULA Kützing, 1844
subtilis Grun.
DIPLONEIS Ehrenburg, 1840
didyma (Ehr.) Ehr.
interrupta (Kütz.) Cl.
var. *interrupta*
var. *caffra* Giffen
pseudovalis Hust.
smithii (Bréb.) Cl.
weissflogi (A.S.) Cl.
EUNOTOGRAMMA Weisse, 1854
laevis Grun. (*laeve*)
FRAGILARIA Lyngbye, 1819
brevistriata Grun.
construens (Ehr.) Grun.
var. *construens*
var. *venter* (Ehr.) Grun.
GOMPHONEMA Agardh, 1824
gracile Ehr.
littorale Hendey
parvulum Kütz.
GRAMMATOPHORA Ehrenberg, 1840
oceanica Ehr.*
GYROSIGMA Hassall, 1845
balticum (Ehr.) Rabh.
beaufortianum Hust.
fascicola (Ehr.) Cl.
hummi Hust.
obliquum Boyer
peisonis (Grun.) Cl.
LICMOPHORA Agardh, 1827
abbreviata Ag.
cf. *debilis* (Kütz.) Grun.
remulus Grun.*
MASTOGLOIA Thwaites, 1856
acutiuscula Grun.*
binotata (Grun.) Cl.
crucicula (Grun.) Cl.
dubia Kütz.
erythraea Grun.*
exigua Lewis
jurgensii Ag.
ovalis A.S.*
pumila (Grun.) Cl.
pusilla (Grun.) Cl.
var. *pusilla*
var. *subcapitata* Hust.*
MELOSIRA Agardh, 1824
nummuloides Ag.
NAVICULA Bory, 1822
abunda Hust.
accomoda Hust.
aequorea Hust.
ammophila Grun.
amphipleuroides Hust.
capitata var. *hungarica* (Grun.) Ross
circumtexta Meister
contenta Grun.
creuzburgensis Krasske
crucicula (W.Sm.) Donk.
cryptocephala Kütz.
cryptolyra Brockman
diserta Hust.
elegans W. Sm.
flanatica Grun.
gregaria Donk.
hudsonis Grun.
hyalinula DeToni

incomposita Hagelstein
var. *incomposita*
var. *minor* Hagelstein
lanceolata (Ag.) Kütz.
marina Ralfs
menisculus Schum.
mutica (Hilse) Grun.
var. *mutica*
var. *stigma* Patr.
nolens Simonsen
obsoleta Hust.
pavillardi Hust.
peregrina (Ehr.) Kütz.
phyllepta Kütz.
platyventris Meister
comoides (Ag.) Perag.
pseudocrassirostris Hust.
pupula var. *rectangularis* (Greg.) Grun.
salinarum Grun.
salinicola Hust.
schroeteri Meister
spicula (Hickie) Cl.
subforcipata Hust.
taraxa Hohn & Hellerm.
tenera Hust.
teneroides Hust.
tripunctata (Müll.) Bory
var. *tripunctata*
var. *schizonemoides* (V.H.) Patr.
yarrenis Grun.
zostereti Grun.
NITZSCHIA Hassall, 1845
amphibia Grun.
angularis W. Sm.
apiculata (Greg.) Grun.
bicapitata Cl.*
bilobata var. *ambigua* Mang.
brittonia Hagelstein
closterium W. Sm.
communis var. *hyalina* Lund
deblis (Arnott) Grun.
dissipita (Kütz.) Grun.
epithemioides Grun.
fasciculata (Grun.) Grun.
filiformis (W. Sm.) Schutt
frustulum (Kütz.) Grun.
var. *frustulum*
var. *perminuta* Grun.
gandersheimiensis Krasske
grana Hohn & Hellerm.
granulata Grun.
hungarica Grun.
lanceolata W. Sm.
lorenziana var. *subtilis* Grun.
minutala Grun.
microcephala Grun.
obtusia W. Sm.
var. *obtusia*
var. *nana* Grun.
palea (Kütz.) W. Sm.
panduriformis Greg.
var. *panduriformis*
var. *continua* Greg.
perversa Grun.
romana Grun.
romanoides Mang.
scalaris (Ehr.) W. Sm.
sigma (Kütz.) W. Sm.
tryblionella Hantz.
vitrea Norman
var. *vitrea*
var. *salinarum* Grun.
OPEPHORA Petit, 1888
parva (Grun.) Krasske
PARALIA Heiberg, 1863
sulcata (Ehr.) Cl.
PLEUROSIGMA W. Smith, 1852.
angulatum (Quek.) W. Sm.
normanii Ralfs
salinarum (Grun.) Grun.
PSAMMODISCUS Round & Mann, 1980
nitidus (Greg.) Round & Mann
RHOPALODIA O. Müller, 1895
gibberula (Ehr.) Müll.
musculus var. *producta* Grun.
STAURONEIS Ehrenberg, 1984
amphioxyis Greg.
var. *amphioxyis*
var. *obtusa* Hendey
legeri Hust.
STRIATELLA Agardh, 1832
unipunctata (Lyngb.) Ag.*
SURIRELLA Turpin, 1828
angusta Kütz.
atomus Hust.
ovalis Bréb.
SYNEDRA Ehrenberg, 1830
affinis Kütz.
fasciculata (Ag.) Kütz.
var. *fasciculata*
var. *intermedia* M. Sullivan
demerarae Grun.
provincialis var. *tortuosa* Grun.*
tabulata var. *parva* (Kütz.) Hust.
THALASSIOSIRA Cleve, 1873
eccentrica (Ehr.) Cl.
leptopus (Grun.) Hasle & Fryxell
TRACHYSPHENIA Petit, 1877
acuminata Perag.*
TROPIDONEIS Cleve, 1891
lepidoptera (Greg.) Cl.
vitrea (W. Sm.) Cl.

GENERAL SUMMARY

A total of 193 taxa (species and their varieties) representing 38 genera comprise the present checklist. Genera with the largest number of taxa are *Navicula* and *Nitzschia* with 46 and 36, respectively. The next most abundant taxa were species of *Amphora* (15), *Mastogloia* (11), and *Achnanthes* (10). Also well represented are *Cocconeis, Cyclotella, Diploneis, Gyrosigma,* and *Synedra* with six taxa each. Eleven taxa were collected only from *Sargassum* in the nearshore waters of southwestern Louisiana.

The present checklist provides important distributional information of an ecologically important group of organisms. Future studies of the varied habitats along the Louisiana coast should result in many new additions to this preliminary checklist.

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A Range Extension for *Manayunkia aestuarina* (Bourne, 1883) (Polychaeta: Sabellidae) to the Gulf Coast of the United States with a Review of Previous Habitat Information

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A RANGE EXTENSION FOR *MANAYUNKIA AESTUARINA* (BOURNE, 1883) (POLYCHAETA: SABELLIDAE) TO THE GULF COAST OF THE UNITED STATES WITH A REVIEW OF PREVIOUS HABITAT INFORMATION

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ABSTRACT The sabellid polychaete *Manayunkia aestuarina* (Bourne, 1883) is reported for the first time from the Gulf coast of the United States and from a *Juncus roemerianus* marsh. Individuals were collected from a brackish *J. roemerianus* marsh in St. Louis Bay, Mississippi, (30°22'N, 89°15'W) during the period of June 1979 to May 1980. Adults with eggs were first noted in early January and increased in number through May. Brooded young were observed from late January through May. Habitat comparisons are made between this and other North American and European populations. The present population is associated with lower salinities, more sandy sediments, and much less frequent tidal inundation than the others. A brief taxonomic discussion is presented.

INTRODUCTION

Two species of the sabellid polychaete genus *Manayunkia* (subfamily Fabricinae) have been reported from the North American continent. *Manayunkia speciosa* Leidy, 1858, has been collected from all coasts of the United States, the Great Lakes region, and from unnamed lakes in northern Alaska (for a review of existing records see Brehm 1978). A second species, *Manayunkia aestuarina* (Bourne, 1883), has been infrequently collected in North America. This species was initially reported on the Atlantic coast by Teal (1962) from Sapelo Island, Georgia, *Spartina alterniflora* marshes where it was the most abundant polychaete. Light (1969), apparently being unfamiliar with Teal's (1962) work, mistakenly claimed that his collection of *M. aestuarina* from mudflats near Vancouver, British Columbia, was the first North American record for the species. Light (1969) suggested that *M. aestuarina* could probably be considered a circumarctic and circumboreal estuarine inhabitant but that a lack of intensive sampling or improper technique had resulted in the true extent of its range remaining unknown. Since the time of Light's (1969) prediction, the occurrence of *M. aestuarina* has been redocumented for the southeastern coast of the United States (Bell and Coull 1978) and for the Pacific coast (Eckman 1979). Bell and Coull (1978) found *M. aestuarina* in the North Inlet estuary, Georgetown, South Carolina, and Bell (1982) subsequently reported on the population biology of *M. aestuarina* from that area (see also Bell 1979, 1980, 1983). Kneib and Stiven (1982) reported effects of predator size on a population of *M. aestuarina* (and other infauna) at Tar Landing marsh in the vicinity of Beaufort, North Carolina. Eckman (1979, 1983) studied the small-scale distribution and recruitment patterns of *M. aestuarina* and other benthos in Skagitt Bay, Washington. The present paper is the first Gulf coast record of a population of *M. aestuarina* and is the first time the species has been found associated with a *Juncus roemerianus* marsh. It is logical to expect that with the current increase of interest in meiofaunal assemblages on all coasts, the presence of *M. aestuarina* will be reported from more localities. Indeed, Heard (1982) suggests but does not confirm the presence of additional populations of *M. aestuarina* in other Gulf estuaries.

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TAXONOMIC REVIEW

Manayunkia aestuarina is a typical representative of the sabellid subfamily Fabricinae Rioja, 1917, which is characterized by minute forms that show a high degree of adaptability to a wide range of intertidal and salinity conditions (Hartman 1951).

This species was first described by Bourne (1883) who erected the new genus *Haplobranchus* for it. McIntosh (1923) alluding to earlier work by Leidy (1858) on *Manayunkia speciosa* cited numerous similarities between the two species and subsequently placed *Haplobranchus aestuarinus* Bourne, 1883, in the genus *Manayunkia.*

Light, in his 1969 report of *Manayunkia aestuarina* from British Columbia, lists two synonyms (*M. polaris* Zenkewitsch, 1935, and *Haplobranchus balticus* Karling, 1934) for this species, at least one of which seems very doubtful. In her work on the Pacific Fabricinae, Hartman (1951) states that *M. polaris* is near *M. aestuarina* but does not explicitly state that the two should be equated. In discussing *H. balticus* however, Hartman (1951) points out that due to differences in number of body segments and setal arrangements this species is not referrable to any named genus in the subfamily. It would seem that because of her extensive work with the group Hartman's view should be given acceptance and *H. balticus* should not be used as a synonym of *M. aestuarina.* That however is simply this author's opinion and any final resolution of the matter will be left to the more qualified professional taxonomists.

TABLE 1

Minimum densities of *Manayunkia aestuarina* and associated environmental data from St Louis Bay, Mississippi

Collection Date	Temperature (°C)			Salinity (ppt)		Sediment		*M. aestuarina* No./m^2
	Air	Water	Soil	Water	Soil	pH	% Organics	
06-29-79	40.0	30.0	24.5	2.0	5.0	4.5	13.22	3
07-30-79	26.5	31.5	25.5	1.0	1.0	4.5	8.10	47
08-23-79	30.0	29.0	25.0	6.0	3.0	5.5	14.96	6
09-23-79	24.0	23.0	23.0	3.0	6.0	6.0	9.51	9
10-29-79	21.0	19.0	14.5	6.0	11.0	5.5	9.02	0
11-30-79	13.0	10.0	8.5	2.0	10.0	6.5	10.47	9
01-04-80	11.0	11.0	9.0	6.0	9.0	6.5	9.48	70
01-26-80	16.0	15.0	13.0	0.0	4.0	6.5	10.63	32
02-23-80	16.0	16.0	15.5	6.0	5.0	6.5	9.07	32
03-22-80	21.5	17.0	13.5	0.0	5.0	6.5	9.90	58
04-26-80	31.0	28.0	23.0	0.0	4.0	6.5	10.85	105
05-23-80	33.0	29.0	24.5	1.0	3.0	6.5	15.30	64

Specimens of *Manayunkia aestuarina* collected from the Mississippi population and deposited with the United States National Museum of Natural History (USNM No. 097391) agree with the detailed descriptions given for the species (Bourne 1883, McIntosh 1923, Fauvel 1927, Light 1969) except for the possibility of a few additional rows of teeth located above the main fang of the thoracic uncini (Fitzhugh personal communication). To avoid repetition, the reader is referred to Bourne (1883) (and the other papers cited) for characteristics and drawings of *M. aestuarina.*

COLLECTION DATA

Specimens of *Manayunkia aestuarina* were collected incidentally during a study of the Mollusca associated with a *Juncus roemerianus* marsh (Bishop 1981). The study was conducted on a small marsh island (30°22′N, 89°15′W) on the western side of St. Louis Bay, Mississippi, during the period June 1979 to May 1980. The marsh was adjacent to tidally influenced Catfish Bayou and the nearby Jourdan River. Considerable information on the study area and past work there is reviewed by Hackney and de la Cruz (1982).

Sampling techniques of the study (Bishop 1981) were designed to quantify macrofaunal organisms and not those species in the meiofaunal size range such as *Manayunkia aestuarina.* Therefore, the numbers of organisms collected should be viewed as minimum estimates only and are presented in Table 1 along with environmental data from each sample date. Bell (1980, 1982) used first setiger width as a measure of size class (i.e. body length) of *M. aestuarina.* In the present study, small individuals (first setiger width $\leqslant$ 0.14 mm) and large *M. aestuarina* (first setiger width $\geqslant$ 0.15 mm) were present in approximately equal numbers in all seasons. Adults with eggs (Berrill 1977) were first noted in the early January sample. The percentage of adults with eggs was greatest in April and May (17% and 27%, respectively). Brooded young were observed from late January through May.

DISCUSSION

Although no quantitative comparisons can be drawn between this population and those of other studies, differences in reported habitat types do emerge. A summary of habitat similarities and differences taken from the literature is presented in Table 2. Entries for European populations represent summaries compiled from a number of sources while East coast (U.S.) information is mainly from the work of Bell (see Table 2 for publication dates).

In Europe, most reports of *Manayunkia aestuarina* give its habitat as unvegetated mudflats from the high intertidal to well within the subtidal zone. It may be present in brackish and low salinity areas, but according to Shütz (1965) it does not occur naturally in areas that lack a marine influence. It is unclear if "does not occur naturally" means total absence or presence only after introduction to such an area. The habitat for *M. aestuarina* as reported by Light (1969) and Eckman (1979, 1983) for Pacific coast populations is the same as for European ones. Both Bell (1982) and the present study indicate that *M. aestuarina* may also be found in vegetated zones of the high intertidal, and Teal (1962) collected many specimens from streamside and levee areas vegetated with *Spartina alterniflora.* The habitat distinctions of vegetated streamside-levee and high intertidal marsh versus unvegetated, intertidal mudflats may represent a lack of collecting in reciprocal areas on these coasts, differences in sampling techniques (e.g. sieve mesh size, lack of staining, etc.), oversight of such a small species or possibly misidentification, and not true habitat differences. Further collections will be required to determine the true range of the spatial distribution of *M. aestuarina.*

The Mississippi population was found to be associated with consistently lower salinities than those reported for other areas (Table 2) and was frequently exposed to bay salinities $\leqslant$ 3.0 ppt (Table 1). Although *Manayunkia aestuarina* is known to exist in areas where brackish to oligohaline conditions persist for short periods of time, such as during

TABLE 2

Habitat comparisons for *Manayunkia aestuarina* from European and North American coastal regions.

Geographic Region	Estimated Density (m^{-2})	Habitat Description	Salinity Regime	Sediment Composition
EUROPE				
Kendall (1979) Muus (1967) Shütz (1965) Light (1969) Zenkewitsch (1957)	From 1.0×10^4 to 1.0×10^6	Mid to high intertidal unvegetated mud flats to 20 m subtidal.	33 ppt (Kendall 1979). Brackish to low salinity but always with marine access. 5–50 ppt (Light 1969).	Mud or muddy with mean grain size of 8 μm. Thin layer of sand in Kendall (1979).
NORTH AMERICA				
Pacific Coast				
Light (1969) Eckman (1979)	"Many" 5.0×10^5	Exposed flats. Flats 2 m above MLLW.	5.0 ppt when collected.	Mud. Thin mud veneer over sand.
East Coast				
Teal (1962)	3.0×10^4	*S. alterniflora* levee marsh.	20–30 ppt.	Undetermined.
Bell and Coull (1978) Bell (1979) Bell (1980) Bell (1982)	1.0×10^5	High intertidal *S. alterniflora* marshes.	"High-salinity estuary."	60–80% silt-clay. 5–10% sand.
Gulf Coast				
Present Report	Undetermined	*J. roemerianus* mid-high marsh.	0–6.0 ppt Bay. 1.0–11.0 ppt Soil.	36.5% sand, 17.5% silt, 46% clay.

spring runoff (Light 1969), the effects of long term exposure to lowered salinities are unknown. Soil salinities in the *Juncus roemerianus* marsh were higher than bay salinities on nine sample dates (Table 1) and could have provided a refuge closer to the more marine salinities reported for *M. aestuarina* (Table 2).

The *Juncus roemerianus* marsh studied is flooded only 12 percent of the time (Hackney and de la Cruz 1978) compared to approximately 25 percent of the time (3–4 hr per tidal cycle) for the South Carolina marsh (Bell 1982) and presumably for other coastal areas experiencing semidiurnal tidal regimes. Since *Manayunkia aestuarina* is a deposit and suspension feeder (Fauchald and Jumars 1979), potential feeding time would be reduced on the irregularly flooded *J. roemerianus* marsh. The effects of such a stress on the abundance, reproductive activity, and general physiological condition of the Mississippi population are unknown and intriguing.

Most reports of *Manayunkia aestuarina* populations are from areas with muddy sediments (but see Eckman 1979, 1983). The soil in the *Juncus roemerianus* marsh was more sandy compared to other studies providing data on sediment composition. Kendall (1979) suggests that *M. aestuarina* is capable of incorporating sand grains in tube construction.

Bell (1982) gives the only data on seasonal recruitment of juveniles for a U.S. population of *Manayunkia aestuarina*. She states that the South Carolina population, unlike European counterparts, exhibits discontinuous recruitment. Also, Bell (1982) states that recruitment of juveniles did not take place in the winter in South Carolina. From observations of brooded juveniles and adults with eggs, recruitment and reproduction in the Mississippi population was also discontinuous but did take place in the winter months. However, adults with eggs were more common in April and May. Early onset of reproduction in the Mississippi population may reflect latitudinal differences between it and the South Carolina population. Increases of soil, air, and water temperatures (Table 1) coincided with the first evidence of juveniles in the *Juncus roemerianus* marsh. Reproductive activity may be triggered in this population by a seasonal warming trend. This type of pattern was also observed (especially in the late spring and summer increases) in the South Carolina population (Bell 1982).

Manayunkia aestuarina is a numerically and perhaps functionally important component of the annelids from this irregularly flooded, low salinity, *Juncus roemerianus* marsh (Bishop 1983). Its ability to survive oligohaline conditions and infrequent inundation is potentially important because such marshes are generally faunally depauperate. The differences noted between the St. Louis Bay, Mississippi, population and those found in other coastal areas of the United States and Europe pose many unanswered questions about the physiological tolerances and exact habitat requirements for the North American populations of *M. aestuarina* and emphasize the fact that we know very little of the basic biology of many non-commercial marsh and estuarine invertebrates.

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Amphipods of the Family Ampeliscidae (Gammaridea). IV. Infraspecific Variation in *Ampelisca agassizi*

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AMPHIPODS OF THE FAMILY AMPELISCIDAE (GAMMARIDEA). IV. INFRASPECIFIC VARIATION IN *AMPELISCA AGASSIZI*

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ABSTRACT Considerable variation noted in *Ampelisca agassizi* is herein described. The variations in the shape of the basis of pereopod 7 and the carina of urosomite 1 are most obvious. No relationship was found with the atypical specimens and their age, associated sediment or location.

One of the most abundant and geographically widespread species of the family Ampeliscidae in the western Atlantic and eastern Pacific Ocean is *Ampelisca agassizi* (Judd 1896). In the western Atlantic this species is recorded from southern Nova Scotia to the Caribbean Sea in depths to 450 m (Barnard 1954b, Mills 1967, Bousfield 1973). Population densities of $15{,}000/m^2$ have been reported by Dickinson et al. (1980) in the Middle Atlantic Bight region. In the eastern Pacific Ocean, representatives of this species have been collected from Queen Charlotte Islands, British Columbia, to Ecuador in depths to 300 m (Dickinson 1982).

Ampelisca agassizi was described from the waters off of the state of Rhode Island in the United States, from pelagic males gathered in a plankton tow and it was originally placed within the genus *Byblis*. Since that work, this species has been described under the names *Ampelisca compressa* Holmes, 1908, from females in the Atlantic and *A. vera* Barnard, 1954, in the Pacific. Mills (1967:645) first designated *A. vera* a junior synonym of *A. agassizi* and noted that "Pacific Coast specimens agree in remarkable detail with those from the Atlantic Coast as J. L. Barnard [1960] has stated and as I have been able to confirm." Recent examinations of representatives of these disjunct populations by Dickinson (1982:6) led that author to write he has "been unable to find a morphological basis for separating the populations on either side of the Isthmus of Panama."

Many *Ampelisca* Kroyer, 1842, species have been reported with transpanamic distributions. A detailed comparison of some of these nominal species has shown the Atlantic and Pacific populations to represent distinct taxa. *Ampelisca bicarinata* Goeke and Heard, 1983, has been separated from the Pacific *A. cristoides* Barnard, 1954, (Barnard 1954a), and *A. parapacifica* Goeke and Heard, 1984, has been shown to be discrete and is separated from *A. pacifica* Holmes, 1908. Atlantic populations of additional "transpanamic" species are yet to be elevated to the species rank (Goeke and Heard, unpublished data).

Variation within the genus *Ampelisca* has been considered a problem by workers in the past. Reid (1951:197) stated "there appears to be a great range of real minor variations which is very strange considering the great constancy of characteristics in many species in other genera." However, Barnard (1960:6) states that he has "identified nearly 10,000 specimens of the 23 species in southern California and is impressed with the ease with which they may be distinguished." He further notes that part of the confusion of workers in the past centered around gerontic males and females. The extreme sexual dimorphism of pelagic males may be disconcerting if not recognized. We agree with Barnard (1960) and note that the western Atlantic taxa are well defined. Much of the confusion arises from suites of closely related species, some of them common but as yet undescribed.

The shape of the seventh leg and the dorsal carina of urosomite 1 are of paramount importance in the systematics of this genus, and minor variation is often attributable to the stage of development of the specimens (e.g., *A. excavata*, Gray and Barnard, 1970). Infraspecific differences noted in *A. agassizi* are not attributable to either developmental stage or location. It is not unusual to examine a group of specimens from a single collection and observe broad variation. For the purpose of this study, material is illustrated from the western, northwestern and southeastern Gulf of Mexico and from off the Atlantic coast of South Carolina.

Pereopod 7 is normally diagnosed for *A. agassizi* as being broad distally. Specimens are often found where the basis is distally rounded (Figure 1K) and not the transversely rounded form figured by Mills (1967:Figure 3J) and Bousfield (1973:Figure 38). This atypical form of leg 7 often makes it difficult to identify the specimen with the use of currently available artificial taxonomic keys. Material which displayed this leg shape came from both the Gulf of Mexico and the East Coast. No relationship was noted with leg shape and developmental stage of the specimens or with sediment.

The variation of the carina of urosomite 1 is not as critical as that noted for the seventh leg because it is often considered a secondary character. The dorsal elevation of the carina varies considerably in height and prominence. The degree of variation in the carina of urosomite 1 is well illustrated by a compilation of figures attributed to *Ampelisca*

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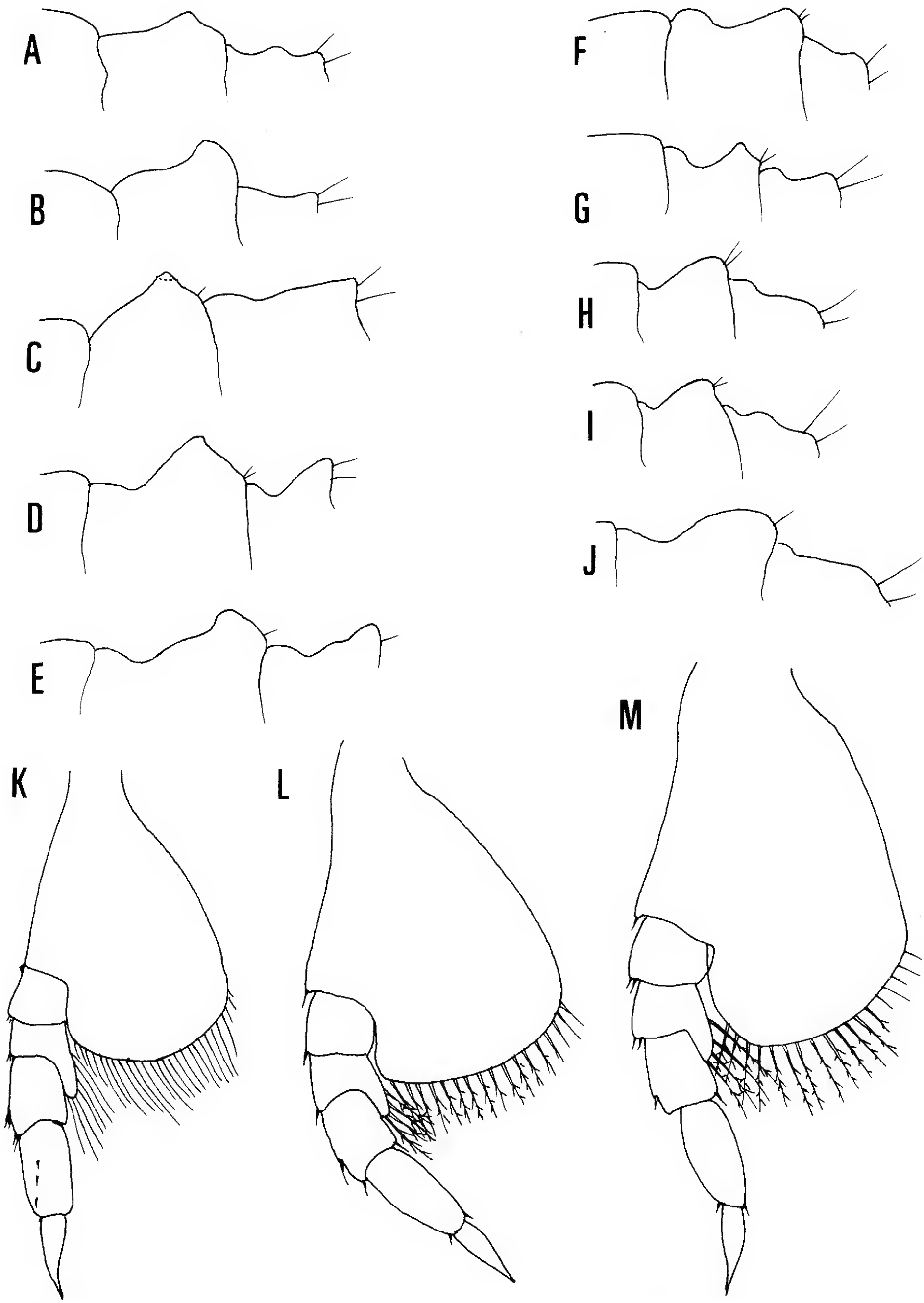

Figure 1. *Ampelisca agassizi;* A. from Dickinson (1982): British Colombia; B. from Barnard (1954a): California; C. from Barnard (1954a): California; D. from Barnard (1954b): Caribbean; E. from Barnard (1954b): Caribbean; F. from Mobile Bay specimen; G. from Mobile Bay specimen; H. from Louisiana specimen with atypical leg; I. from Louisiana specimen with atypical leg; J. from Bousfield (1973): New England; K. from Barnard (1954a): California; L. from Louisiana specimen; M. from Louisiana specimen with atypical leg.

agassizi from the Pacific and Atlantic (Figure 1A–J). These have been gathered from various sources and represent a very broad geographic range. None of the Atlantic material examined by these authors has any indication of a second elevation on the fused urosomite 2–3 as shown by Dickinson (1982:Figure 1) for material from British Colombia. No relationship with the stage of development, sediment or leg shape and form of carina was indicated.

The atypical specimens examined by us were also checked for variation in other important taxonomic characters. No significant variation was noted in antennal features, structure of mouthparts or pereopods 1–6.

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